DRY WOODLAND AND SAVANNA VEGETATION DYNAMICS IN THE EASTERN OKAVANGO DELTA, BOTSWANA

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ABSTRACT

The Okavango Delta is an extremely dynamic system with variable vegetation comprised of permanent swamps, seasonal swamps, dry islands, floodplains and dry grassland, savanna and woodland. The system is largely driven by the interaction between fire and the annual flood, which filters down from the Okavango River catchments in Angola. While extensive research has been conducted on the flood-driven vegetation little is known about the dry woodland and savanna regions bordering these flood-driven habitats. A taxonomic classification of woody species composition resulted in eleven vegetation types. These data were then reanalyzed in terms of woody species morphology allowing these eleven vegetation types to be grouped into four functional response groups in order to provide a platform for improving the understanding of how dry woodland and savannas interact with the environment. These four groups were the savanna group mixed thornveld and the three woodland groups; mixed broadleaf woodland, shrub mopane woodland and tall mopane woodland. Burning in mixed thornveld and mixed broadleaf woodland was found to decrease woody species density and grass fuel loads and could be used for grazing management to remove unpalatable growth and improve grass species composition, while burning in shrub mopane woodland and mixed mopane woodland merely decreased the woody understory and is not recommended. Utilization dominated by grazing livestock resulted in overutilization of the grass sward leading to bush encroachment in both mixed thornveld and shrub mopane woodland, while utilization by goats alone resulted in underutilization of the grass sward and a dominance of herbaceous annuals. Livestock utilization had no effect on the occurrence of *Pecheul-loeschea leubnitziae*, a shrubby pioneer previously thought to be an indicator of overgrazing, however extensive *P. leubnitziae* cover was associated with a sward dominated by shade-tolerant grasses with low forage quality. Shrub mopane woodland and tall mopane woodland appear to be more stable vegetation states than mixed broadleaf woodland and mixed thornveld being less vulnerable to colonization by pioneer species and alteration as a result of utilization or environmental factors. For this reason management and monitoring of mixed thornveld and mixed broadleaf woodland is essential to prevent vegetation degradation and to ensure optimal forage availability for both livestock and wildlife.

PREFACE

This thesis is the result of the author's original work except where acknowledged or specifically stated to the contrary in the text. It has not been submitted for any degree or examination at any other university or academic institution.

Signed …… Date ……/……/……

Michelle Jennifer Tedder

Signed …… Date ……/……/……

Prof. Kevin Kirkman (supervisor)

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CHAPTER 1: INTRODUCTION

1.1 THE OKAVANGO DELTA

The topography of Botswana is largely influenced by the East African Rift System. This rift originates in the Red Sea and extends southwards into northern Malawi where it splits into two branches. The western branch extends south-west through Zambia and into northern Botswana. This rift results in two depressions separated by the Ganzi Ridge. One depression contains the Okavango Delta and the other the Makgadigadi Pans (McCarthy and Ellery 1998) (Figure 1.1).

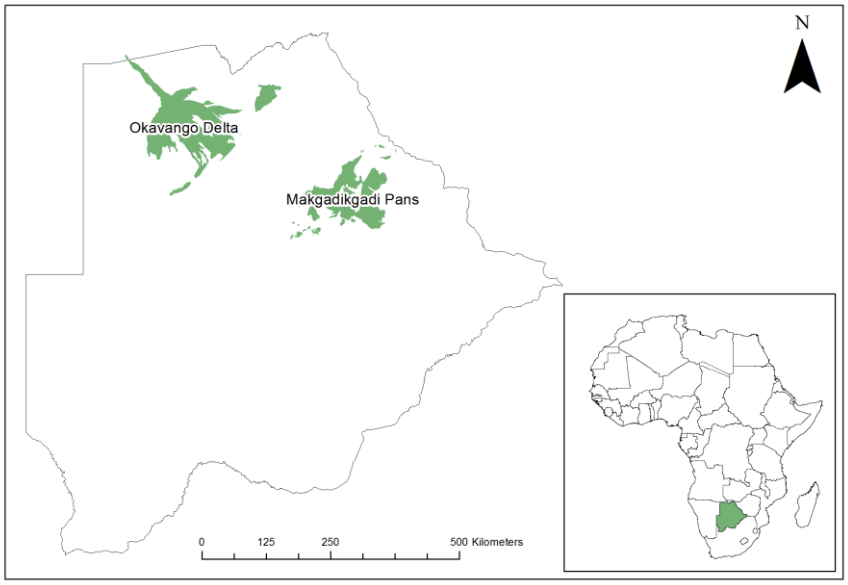

Figure 1.1: Map of Botswana showing location of Okavango Delta and Makgadikgadi Pans.

The Okavango Delta is situated in the Ngamiland district (Heinl et al. 2006) and bordered by Namibia and the Caprivi Strip. It is one of the world's largest inundated deltas covering between 30 000 and 40 000 km^2 (McCarthy and Ellery 1994, McCarthy et al. 2003) and is the world's fifth-largest Ramsar site (Ramsar-Convention-Secretariat 2011). The area is flooded annually when rainwater from catchments in the Angolan highlands flows into the Cubango and Quito Rivers. In north-eastern Namibia these two rivers join to form the Okavango River. The Okavango River then flows into the Panhandle region of the Okavango Delta. The flood water arrives in April and results in a rise in water level of approximately 2m. This water is contained between skarps, caused by two fault lines running from North-West to South-East, as it flows down the Panhandle region of the Delta (Heinl et al. 2008). This section of the Delta has a gradient of 1:5500 (McCarthy and Ellery 1998). These two fault lines then meet the Gomare fault line running from the North-East to the South-West (Bailey 1998). At this point the Panhandle feeds into three

channels, the Nqoga which flows east and takes 63% of the Panhandle outflow, the Jao which flows south-east and takes 21% of the Panhandle outflow and the Thaoge which flows south and takes 16% of the Panhandle outflow (McCarthy and Ellery 1998). Originally the Thaoge was the main distributary channel for the Panhandle outflow but in the 1880s the flow shifted east making the Nqoge the primary channel (McCarthy and Ellery 1998). The Nqoga feeds into the Khiandiandava and Maunachira, which in turn feeds into the Mboroga and Santanadibe. These channels are separated by sandveld tongues, with Chief's Island separating the Jao and Nqoga, and are lined with peat which is supported by the surrounding vegetation allowing water to seep out of the main channels (McCarthy and Ellery 1998).

The water then begins to spread out forming the Fan region of the Delta (Bailey 1998, Heinl et al. 2008). The gradient here increases to 1:3300 (McCarthy and Ellery 1998). The flooding in this region of the Delta is largely unconfined extending over large areas and causing little to no rise in water level (McCarthy and Ellery 1998, Heinl et al. 2008). At the lower reaches of the Fan the water level rises again as the floodwaters meet the Thamalakane fault which forms a 12m skarp and defines the course of the Thamalakane River (McCarthy and Ellery 1998).

These regions remain flooded from May to September (McCarthy et al. 2003). The maximum extent of the flooded area varies annually from as little as 5 000 km^2 up to 15 000 km^2 (McCarthy et al. 2003, Heinl et al. 2008). The smallest inundated area recorded in the last 30 years was recorded in 1996 with only 5094 km^2 underwater at the peak of the flood (McCarthy et al. 2003). There is little outflow from the Okavango Delta system as 96% of the water is lost to evapotranspiration (McCarthy and Ellery 1998). Of the remaining water only 2% leaves as ground water outflow and 1.5% flows out of the system, via the Tamalakane, into the Boteti River (McCarthy and Ellery 1998). In years with high flood waters the river flows into Lake Xau and then on into Ntwetwe Pan on the western side of the Makgadikgadi Pans (Ellery and McCarthy 1998).

1.1.1 River Systems

Owing to the presence of fault lines running through and around the Delta (Figure 1.2), earth tremors are fairly common. Although these tremors are not generally strong enough to result in major structural damage they are sufficient to alter the topography of the region and, owing to the low elevation gradient within the Fan region, alter the flow of streams and rivers (Johnson and Bannister 1977). Between the early 1950s and the late 1970s several earthquakes of significant extent were recorded (Bailey 1998) and many of these have been correlated with changes in the pattern of flooding (Rűbbel and Child 1976, McCarthy and Ellery 1998).

One such change was that the Boro River, which had been dry for 30 years, began to flow again and continues to flow today (Johnson and Bannister 1977). Rűbbel and Child (1976) also mention an anonymous report published in 1972 that attributes the drying of the lower regions of the Khwai River and Mogogelo River, a tributary of the Gomoti River flowing towards the south-east, to seismic activity. Researchers in the lower Mogogelo area have also observed what appear to be man-made blockages in the dry river channel which may further prevent water flow to its lower reaches (Cozzi 2010 personal communication). Until the 1950s the 65 km long Gomoti River was a major outflow of the annual flood into the south eastern regions of the Okavango Delta (Bernard and Moetapele 2005). Since then the channel collects only rainwater and those people who depended on the river for survival have moved away (Bernard and Moetapele 2005).

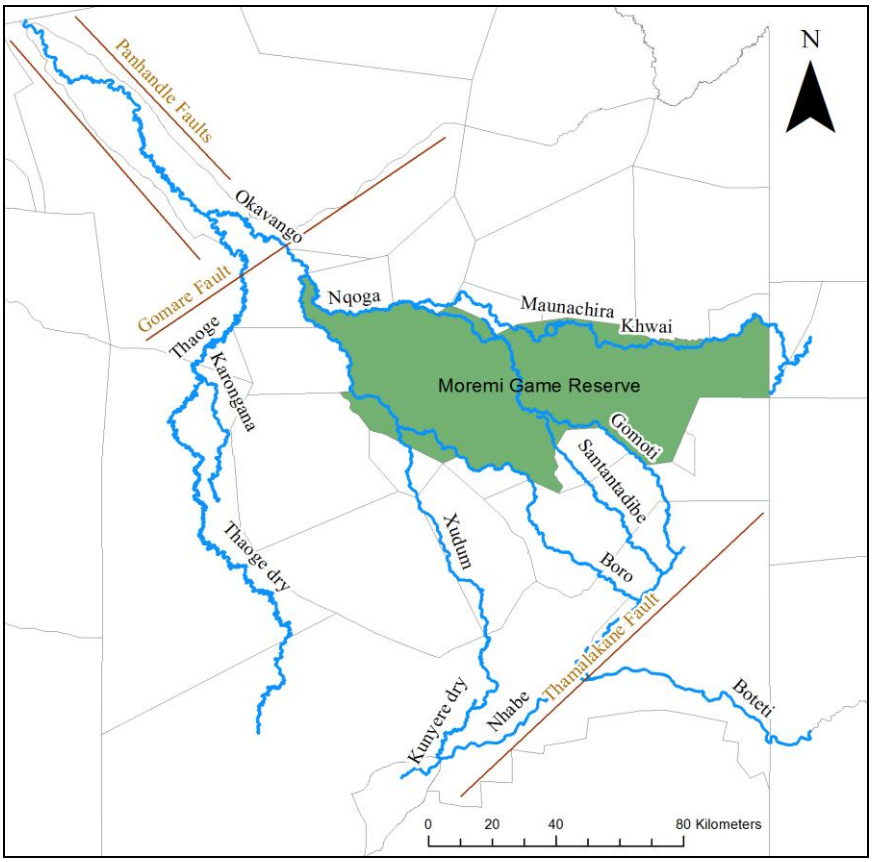

Figure 1.2: Map of the rivers and channels (blue) of the Okavango Delta showing primary fault lines (brown) and wildlife management area boundaries (grey).

There are records that in 1904 the Mababe section of the Moremi Wildlife Reserve was a swampy area with the perennial Mogogelo River flowing so strongly, that in order to pass through the area wagons had

to be floated across it and oxen swum across (Rűbbel and Child 1976). Since 1938 the majority of these floodplains have disappeared with the most conspicuous changes taking place near old settlements where there were large numbers of livestock (Rűbbel and Child 1976). McCarthy & Ellery (1994) and Ellery & McCarthy (1998) now indicate the region extending to the north-east of the Gomoti River as a seasonal swamp. Dr Tico McNutt, Director of the Botswana Predator Conservation Trust, has also stated that when his research in the area first started in 1989 the section of the Mogogelo river near Santawani Camp had water in it (McIntyre 2008). This riverbed is currently dry (personal observation, 2010).

1.1.2 Community

1.1.2.1 Population

In late 1970s there were approximately 40 000 people living in and around the Delta. This population comprised several different tribes, namely the Banoka, Bayei, Hambukushu, Batwana, Bangwato, Bakalahari and Ovaherero. Seventy percent of these people owned no cattle and earned no salary but survived by living off the natural resources provided by the Delta. The Banoka or River Bushmen are the original inhabitants of the area and are believed to have been living along and fishing the channels of the Delta for about 100 000 years. The Bayei, Hambukushu, Batwana, Bakalahari and Ovaherero all migrated into the area within the last 250 years. The Hambukushu were agro-pastoralists and the Bayei fisherman became hunter-gathers after settling on the shores of lake Ngami south of the Okavango Delta, while the Batwana, Bangwato and Ovaherero were predominantly cattle farmers, with the Ovaherero being some of the wealthiest cattle farmers in the region today (Johnson and Bannister 1977, Bailey 1998). Today approximately 25% of Botswana's population are of Bangwato descent (Johnson and Bannister 1977) but despite the 26 different languages spoken in the country most inhabitants identify themselves as Batswana or Matswana, meaning the people of Botswana (McIntyre 2008).

1.1.2.2 Cattle Industry

With the arrival of the Batwana, Bagwato and Ovaherero there was a marked increase in the number of cattle farmers in Botswana. This trend follows today with the Bagwato, a cattle farming people, comprising one quarter of Botswana's population. Originally the movement of the cattle farming tribes and the size of their herds was restricted by water availability, but increasing numbers of boreholes in community grazing land have made additional grazing available resulting in increasing land utilization and herd sizes (Bailey 1998).

In the 1950s in an attempt to control the recurring outbreaks of foot and mouth disease, resulting from the rapidly increasing herd sizes, three veterinary cordon fences were built effectively cutting the country into

four blocks (Hannah et al. 1988). In 1958 a fourth inland fence, the Kuke fence, was built denoting the southern boundary of Ngamiland (Hannah et al. 1988, Harrison 2006). Additional fencing was later constructed in the central district and the western, southern and eastern borders of the Okavango Delta to prevent the foot and mouth carrying buffalo from coming into contact with domestic cattle (Hannah et al. 1988).

1.1.3 Protected Areas

The present day Botswana Department of Wildlife and National Parks was originally founded in the late 1950s, as an Elephant Control Unit, with the purpose of protecting crops and water resources in the Tati and Tuli-Block regions from elephants crossing into Botswana from Zimbabwe (Molosiwa 1999). In 1961 the unit was renamed the Game Department and in conjunction with the introduction of the Fauna Conservation Proclamation Act No. 22 of 1961 began regulating hunting licenses (Molosiwa 1999). In 1968 the Game Department was then renamed the Department of Wildlife and National Parks and Tourism and the National Parks Act was passed. The department now works under the Wildlife and National Parks Act No. 28 of 1992 which combines the Fauna Conservation Act and the National Parks Act. In 1999 41 % of the land in Botswana had been allocated to the management and protection of wildlife, with 24% as Wildlife Management Areas and 17% as game reserves and national parks.

Botswana has 7 declared game reserves and 4 national parks (Molosiwa 1999). The national parks are registered under IUCN category II. These areas have been declared by the head of state and all forms of hunting and plant and animal collecting is forbidden. The game reserves are registered under IUCN category IV and hunting is forbidden without the possession of a valid permit (Campbell 1973, Hannah et al. 1988).

1.1.3.1 Moremi Game Reserve

Moremi Game Reserve is Botswana's second largest game reserve and was proclaimed in 1963 through the Fauna and Flora Preservation Society of Ngamiland, by the Batwana people to protect the wildlife in the area. The reserve was 2 000 km^2 and was the first official reserve on tribal land. The area was selected for its varied habitat, easily visible boundaries provided by the Mogogelo and Khwai Rivers and the lack of human population in the area (Figure 1.3). Chief's Island was proclaimed in the late 1970s and added to Moremi Game Reserve (Harrison 2006).

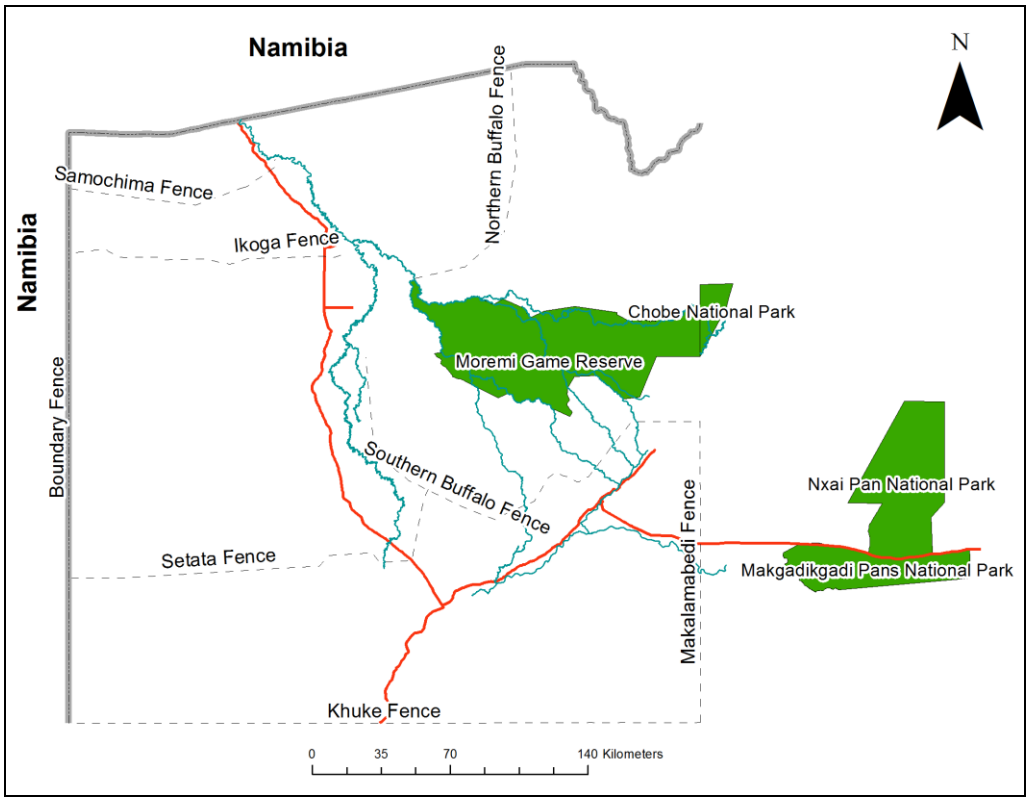

Figure 1.3: Game Reserves and National Parks of Ngamiland showing veterinary cordon fences. Major roads are indicated in red.

1.1.4 Wildlife Tourism

Wildlife and nature-based tourism account for approximately 60% of global international tourism annually. In Botswana tourism contributes 6% to the annual Gross Domestic Product (GDP) (Harrison 2006), four times more than the beef industry (Bailey 1998), and approximately 53% of the population derives some form of income from it. In the mid-1990s the number of tourists visiting Botswana's northern Parks was doubling annually (Bailey 1998) and the Okavango remains the most popular tourist destination in Botswana being visited by approximately 800 000 foreign tourists each year (Harrison 2006).

1.1.5 Community Based Natural Resource Management

The development of Community Based Natural Resource Management (CBNRM) in southern and east Africa began in the 1980s. The driving forces behind the development of this program were as follows; the threat of species extinction as a result of poaching and overutilization, the inability of the state to effectively protect the countries natural resources, accelerating land use conflicts between communities

living in resource areas and the resource managers overseeing the areas and the need to create a link between conservation and community development (Mbaiwa 2004, Harrison 2006).

The Wildlife Conservation Policy of 1986 and the Tourism Policy of 1990 paved the way for the development of CBNRM in Botswana (Mbaiwa 2004, Harrison 2006) proposing the division of all nine districts in Botswana, Ngamiland, Chobe, Ghanzi, Central, North-East, Kweneng, Kgatleng, Southern and Kalagadi, into Wildlife Management Areas (WMA). The WMAs were then further divided into Controlled Hunting Areas (CHA). These WMAs allow for conservation and controlled utilization of wildlife outside of the national parks and game reserves and in addition provide a buffer zone between protected areas and surrounding human settlement. The Okavango Delta is divided into 28 WMAs which are further divided into a total of 49 CHAs (Mbaiwa 2004).

1.1.6 Okavango Delta Management Plan

In 1997 when Botswana ratified the Ramsar Convention, the Okavango Delta and its surrounding areas, encompassing the Tsodilo hills, Lake Ngami and the Kwamdo and Linyanti river systems, were declared a Ramsar site or wetland of international importance (Trollope et al. 2006, Magole et al. 2009). The purpose of this convention is to ensure 'the conservation and wise use of all wetlands through local and national actions and international cooperation, as a contribution towards achieving sustainable development throughout the world' (Ramsar-Convention-Secretariat 2006).

In the same year as the Ramsar site was declared, a wetlands conference was held in Maun in order to formulate a list of wetland policy issues. This initiated the process resulting in the publication of a draft National Wetlands Policy and Strategy in 1999 (Jansen and Madzwamuse 2003). Along with the identification of the major factors contributing to wetland degradation the policy highlights the importance of the development of management plans for all nationally important wetlands and Ramsar sites (Jansen and Madzwamuse 2003). As a result of this the Okavango Delta Management Plan (ODMP) proposal was drawn up in 2002 (Trollope et al. 2006) with the primary objective being 'to integrate resource management for the Okavango Delta that will ensure its long term conservation and that will provide benefits for the present and future well-being of people, through sustainable use of its natural resources' (Jansen and Madzwamuse 2003). The proposal identified the following ten project components and the agencies responsible for them; policy, planning and strategy, research, data management and training, hydrology and water resources, wildlife management, sustainable tourism, fisheries and animal health, vegetation resources, physical planning, land-use planning and land management and local authority services provision. The responsibility for research, data management and training falls to the

Okavango Research Institute, while the responsibility for the vegetation resources component falls to the Department of Forestry and Range Resources (DFRR) (Jansen and Madzwamuse 2003).

As there is currently little direct management of the vegetation component of the Okavango Delta numerous problems have been identified to be addressed within the framework of the ODMP. These issues can be grouped into five categories; issues relating to human induced factors, natural factors, lack of or poor information or consultation, land use factors and management of resources (DFRR 2011). Some of the outcomes which the DFRR hopes to achieve by addressing these problems are as follows; to carry out a vegetation classification and map vegetation cover, to assess vegetation resource use such as grazing and wood harvesting, to identify vegetation resource monitoring sites and design a monitoring programme, to establish fire monitoring sites and to study invasive species (DFRR 2011).

1.2 VEGETATION OF THE OKAVANGO DELTA

Despite covering an area of only 25 000 km^2, a mere 4% of Botswana, the Okavango Delta is host to 65% of the plant species occurring in the country (Ramberg et al. 2006). This richness and diversity of species results from the mosaic of habitats created by the annual floodwaters which flow into the Delta from the catchments in the Angolan highlands (McCarthy and Ellery 1998, Ramberg et al. 2006). These floodwaters create an intricate mosaic of permanent swamps, seasonal swamps, occasional wetlands (regions which flood at approximately 10 year intervals) and dry islands. While much of literature on the vegetation of the Okavango Delta is focused on two main categories, namely the permanent and the seasonal swamp vegetation (McCarthy and Ellery 1998, Rogers 2003), some authors break this grouping down further to include the permanent swamps, seasonal swamps and occasional wetlands (Ellery and Ellery 1997, Gumbricht et al. 2004, Ramberg et al. 2006). The occasional wetlands are estimated to cover 7100km^2, an area 20% larger than that of the permanent swamps (2500 km^2) and seasonal swamps (3300 km^2) combined (Ramberg et al. 2006).

1.2.1 Vegetation Communities

Within the permanent swamp areas there are the upper and lower permanent swamps with their associated back swamp regions (Rogers 2003) and within the seasonal swamps and their associated floodplains there are dry islands, strips of riparian vegetation lining the floodplains and edges of the dry islands, drainage lines, old drainage lines, *Terminalia* thicket, *Acacia erioloba* woodland and *Mopane* veld (Ellery and Ellery 1997).

The permanent swamps comprise three main plant communities; tall emergent communities, characterised by *Cyperus papyrus, Miscanthus junceus* and *Phragmites australis*, short emergent communities, characterised by a diverse cohort of grasses and sedges with an abundance of *Pycreus nitidus* and open water communities, characterised by water lilies (*Nymphaea* sp.), sedges (*Eleocharis* sp.), *Brasenia schreberi* and *Nymphoides indica* (McCarthy and Ellery 1998). Tall emergent communities occur in the upper permanent swamps where the channels are fast flowing and largely devoid of vegetation. These channels flow through *C. papyrus* communities with an understory of *Thelypteris interrupta*. In the shallower, slower flowing channels of the lower permanent swamps the short emergent communities occur with various submerged open water plant communities, such as *Eichhornia natans*, *Ottelia ulvifolia*, *Potamogeton octandrus* and *Rotala myriophylloides*, found in the channels themselves. In the back swamps of the lower permanent swamp regions the open water plant communities are comprised of a combination of submerged species, such as *Ceratophyllum demersum* and *Lagarosiphon ilicifolius*, and floating leaf species such as *Brasenia nitidus* and *Nymphaea nouchali* var. *caerulea*. These back swamps also have mats of floating vegetation which provide colonization opportunities for emergent species such as *Pycreus nitidus* and *Leersia friesii* (Rogers 2003).

Species distribution in the seasonal swamps is dependent on the depth and duration of inundation during flooding. Vegetation communities in low-lying areas which are flooded for extended periods of time are comprised of plants with floating leaves analogous to those found in the open water regions of the permanent swamps, as well as sedge species such as *Cyperus articulatus* and *Schoenoplectus corymbosus* and grasses such as *Echinochloa* spp. As the elevation increases and the duration of inundation decreases grass and sedge species such as *Leersia hexandra* and *Oryza longistaminata* increase in abundance, with the upper floodplain regions being dominated by wet site adapted grasses such as *Imperata cylindrica* (McCarthy and Ellery 1998). Moist, loamy soils tend to be characterised by *Eragrostis rigidior*, *Panicum repens*, *Cyperus esculentus*, *Leersia* species, *Paspalum* species, *Echinochloa* species and *Vossia* species while dry sandy soils are dominated by *Cynodon dactylon, Chloris virgata*, *Melinis repens*, *Cymbopogon excavatus*, *Hyparrhenia rufa* and *Eragrostis viscose* with *Sporobolus spicatus* restricted to the white powdery saline soils (Ellery and Ellery 1997). The species diversity of these active floodplains is higher than that of the drying floodplains (Heinl et al. 2007). *Acacia nigrescens* is a characteristic tree on the drying floodplains while *Acacia erioloba* dominates on the sandy alluvium. *Colophospermum mopane* is present on poorly drained soils with a compacted layer below the surface (Cole 1982). Within *C. mopane* dominated vegetation two structural morphs have been observed. Tall single-stemmed *C. mopane* trees occur on moist, alluvial soils, while short, shrubby individuals occur on drier, sandy soils. These short

trees are vulnerable to defoliation and fire resulting in multi-stemmed coppice growth (Roodt 1998, February et al. 2007).

These flood-driven habitats are bordered by a substantial belt of dry woodland vegetation which surrounds the Delta (Mendelsohn and el Obeid 2004). Many of these regions have never been flooded, while others have become dry as a result of seismic shifts and changing flooding patterns (Rűbbel and Child 1976, Johnson and Bannister 1977, McIntyre 2008). This drying, coupled with the associated changes in fire regime and herbivory, has led to the development of rain-fed semi-arid bush dominated by stands of mature woody species which would not be able to withstand regular inundation where previously floodplains occurred (Tang and Kozlowski 1989, Ringrose et al. 2005). Of the 1300 plant taxa recorded in the Okavango Delta, 60% occur in these dry woodland regions (Ramberg et al. 2006).

1.2.2 Factors Affecting Vegetation Distribution

1.2.2.1 Soils

In undisturbed vegetation a decrease in soil moisture and available nutrients will be accompanied by a natural progression from tropical forest to savanna. Tree, shrub and grass height and spacing are dictated by soil moisture, while species composition varies with soil nutrient status. Both soil moisture and soil nutrient levels are dependent on the soil parent material of bedrock geology, superficial deposits such as windblown sand, alluvium and colluviums and weathering products such as laterite and calcrete (Cole 1982).

The savannas in Botswana generally occur in valleys floored by Karroo rocks buried under alluvial deposits and are characterized by black cracking clays. Savanna woodlands occur on old alluvial deposits, while low tree and shrub savannas are found on a base of Kalahari sand. In regions where the alluvium is silty sand, *Acacia tortilis* dominates, while in the sandier regions *Acacia erioloba* dominates and *Acacia erubescens* with a grass layer comprised of S*chmidtia pappophoroides, Eragrostis horizontalis* and *Aristida hordeacea* occurs over Karroo basalt. *Combretum apiculatum* with a grass layer dominated by *Stipagrostis uniplumis* occurs on reddish sandy soils, while mixed stands of *C. apiculatum, Terminalia prunoides* and *Commiphora pyracanthoides* are associated with calcrete development (McCarthy and Ellery 1998, Roodt 1998).

1.2.2.1.1 Particle size and density

Soil particle size results from the type of parent material from which a soil is derived. This factor affects a wide range of soil properties such as aeration, infiltration or the ability for water to move from the soil

surface into the topsoil layer, water storage and soil fertility (Miller and Gardiner 1958). Sandy soils have large pores between the soil particles and thus have good aeration and infiltration, however they have poor water storage capacity, drying quickly and losing soluble nutrients which leach down the soil profile. Soils with a high clay content tend to be more fertile as they hold nutrients and soil water more effectively (Miller and Gardiner 1958). The extent to which these clay soils absorb soluble cations is dependent on the percentage clay content of the soil, the mineralogy of that clay and percentage and type of organic matter found in the soil. These soils are however prone to waterlogging in high rainfall regions resulting in soil oxygen shortages (Wild 1993). Extended waterlogging may also result in increased soil acidity and high levels of phytotoxic chemicals produced in anaerobic soil (Wild 1993).

1.2.2.1.2 Nutrient content and pH

High levels of rainfall for extended periods also result in the leaching of calcium, magnesium, sodium and potassium cations thus decreasing soil nutrient levels and lowering soil pH (Bonyongo and Mubyana 2004). These basic cations are replaced by protons and aluminum ions which are toxic to plants and soil microbes. Absorption of these aluminum ions results in decreasing cell division and root elongation with roots becoming restricted to the upper soil layers making plants more prone to drought (Miller and Gardiner 1958, Wild 1993, Bardgett 2005). This increase in soil acidity also decreases organic matter decomposition rates resulting in decreased levels of nitrogen, phosphorus and sulphur, further decreasing the soil nutrient levels. In addition the nitrogen-fixing ability of legumes may be inhibited unless the *Rhizobium* strain present is acid tolerant (Miller and Gardiner 1958, Wild 1993).

1.2.2.1.3 Flooding and soils

The floodwaters of the Okavango Delta deposit cations such as, phosphorus, calcium and magnesium into the floodplain soils. These cations deposited into the floodwaters by decaying plant debris increase the salinity of the soil thus increasing the soil pH (Bonyongo and Mubyana 2004). Bonyongo and Mubyana (2004) found the soils close to the river channel to be rich in phosphorus, calcium and magnesium, while the more soluble cations such as potassium and sodium are found in greater density further away from the river channel. The source of these minerals is generally fire debris which has been transported by the floodwaters or deposited by local fires (Bonyongo and Mubyana 2004).

1.2.2.2 Fire

1.2.2.2.1 Fire and Vegetation

Fire is a common occurrence in the savannas of Africa, South America, Asia and Australia (Higgins et al. 2000). Local communities have been burning African grassland and wetland areas for as long as 55 000

years (Heinl et al. 2007). These fires were used as a management technique to improve the quality of cattle grazing areas, to attract wildlife for hunting, to clear land adjacent to channels to allow for flood-recession farming and to clear access routes to fishing grounds (Bernard and Moetapele 2005, Heinl et al. 2007). Despite burning being prohibited, there is to date, still a high frequency of fires in the Okavango Delta creating a mosaic of burnt and unburnt patches which interact with flooding patterns to influence vegetation patterns (Heinl et al. 2006). It is thought that the majority of these fires have anthropogenic origin, such as campfires, fish smoking and honey collection, as there is little lightning activity during the fire season to cause natural ignitions (Heinl et al. 2008).

1.2.2.2.2 Fire frequency

Fires in dryland regions tend to burn a large area but occur at low frequency, with a mean fire return interval of approximately 22 years, while floodplain fires cover small areas but occur frequently, with a mean fire return interval of 7 years. The frequency of floodplain fires is determined by flooding frequency. Frequent flooding results in a larger fuel load and greater fire frequency. However a flooding frequency greater than biennial suppresses fire, as large areas remain inundated and the fuel load does not dry sufficiently (Heinl et al. 2006). Dryland fire frequency is strongly related to annual rainfall and is also correlated to the proximity of the area to floodplains which increase water supply to the area and thus increase biomass (Heinl et al. 2006). Floodplains generally burn early in the dry season just before flooding, while the drylands burn late in the dry season just before the first rains (Heinl et al. 2007).

1.2.2.2.3 Effects of fire on vegetation

A substantial proportion of the species occurring in southern Africa are fire tolerant species. Savannas occur where the fire intensity is sufficient to limit the recruitment of seedlings into the adult tree layer but not so intense as to prevent it completely. These savanna species can survive varied environmental conditions and have the ability to re-sprout from the underground rootstock when the aboveground stem is killed by fire. This ability is called the ‘gulliver effect’ (Bond and Van Wilgen 1996). These trees may be several years old but are kept in a stunted state by repeated burning. Escape from the grass layer and thus from the zone of intense fire depends on the fire frequency and stem growth, with taller, thicker plants with a thick bark layer being able to survive fires better than the shorter thinner plants (Higgins et al. 2000). Low fire frequencies allow tree seedlings to escape the grass layer resulting in an increase in woody plant density, while high fire frequencies result in an increase in herbaceous plant density, while decreasing the available fuel load and thus decreasing the flame intensity and height which increases the survival rate of large trees (Heinl et al. 2008). In addition season of burning plays a role in the effects of fire on the vegetation. Burning in late spring and early summer after the grass sward has begun actively

growing may result in severe damage to the growing points, while burning in winter results in an early flush of growth which may protect the soil surface from erosion (Trollope 1999).

Species composition on active floodplains is determined by frequency of flooding as fires usually occur in June when the rhizomatous floodplain species are dormant and the rhizomes are protected by accumulated dry matter (Heinl et al. 2008). Of the species affected by fire *Cyperus denudatus*, *Eragrostis lappula* and *Setaria sphacelata* are positively affected, while *Cyperus articulates* and *Eclipta prostrata* are negatively affected. On the drying floodplains *Cynodon dactylon* is also negatively affected showing a decrease in cover percentage with increasing fire frequency. In addition drying floodplains show an increasing woody species density, however if fire frequency increases as the floodplain dries, woody species density decreases and a low cover abundance for large trees, such a *Combretum imberbe*, is observed. Both *Colophospermum mopane* and *Pechuel-loeschea leubnitziae*, which were only observed in the drying floodplains, have been observed to resprout after burning (Heinl et al. 2008).

1.2.2.3 Flooding

1.2.2.3.1 Flooding frequency

From 1989 to 2003 75.4% of the southern Okavango Delta remained unflooded. Owing to a large flood in 1989 7.5% of the area flooded once and did not flood again until 2003. The remaining 17.1% flooded between 2 and 15 times with none of these flood frequency categories contributing more that 2.7% to the total (Heinl et al. 2006).

1.2.2.3.2 Effects of flooding on vegetation

Studies have shown that flooding for periods as short as a few weeks can retard plant growth. This inundation results in a decrease in stem elongation, leaf growth, cambial growth, reproductive growth, shoot elongation, leaf initiation, leaf expansion and root growth, and an increase in leaf senescence, plant injury and leaf abscission (Tang and Kozlowski 1982). Waterlogged crops have shown a decrease in yields if flooded for more than a few days (Leeper and Uren 1993) and a study by Tang and Kozlowski (1989) showed that seedlings of *Betula papyrifera* which had been flooded had 75% less leaves after 60 days than the seedlings which had not been flooded (Tang and Kozlowski 1982).

These plant responses to flooding result from a decrease in soil aeration (Anon 2008), as a result of large air spaces filling with water and thus slowing oxygen conduction by 10 000 times (Leeper and Uren 1993), an increase in the pH of acidic soils and a decrease in the pH of alkaline soils and a decrease in organic matter decomposition rates. In addition sedimentation from floodwaters further decreases soil

aeration and smothers smaller trees. High concentrations of ethanol and hydrogen sulphide are produced in waterlogged soils and attack by secondary fungi further contribute to the root damage resulting from flooding (Anon 2008). These anerobic conditions resulting from waterlogging also result in soil denitrification, where plant-available nitrates are converted to un-useable nitrites, and unsoluble manganese and iron oxides are converted to soluble ferrous and manganous ions which at high levels are toxic to plants (Leeper and Uren 1993).

Tall trees with the majority of the crown out of the water and adult trees are more likely to survive extended flooding (Anon 2008). Flooding during the growing season is least harmful to tree growth, although plants are the most vulnerable to flood damage just after the leaf flush of the season. These plants can withstand between one and four months of flooding but not recurrent flooding where the soil remains waterlogged. Plant survival is improved if the water is flowing rather than stagnant as it improves the soil oxygen content (Anon 2008). Some plant species have adapted to develop new adventitious roots to compensate for the loss of fine absorbing roots. These roots increase water absorption by up to 90%. In addition to this the aerial tissues increase oxygen absorption which diffuses out the roots and oxidizes toxic reduced compounds such as ferrous and manganous ions (Kozlowski 1985).

1.3 IMPACTS OF LAND USE ON VEGETATION

1.3.1 Wildlife utilization

1.3.1.1 Elephant

Elephants comprise seventy percent of the total wildlife biomass in the Moremi Game Reserve and surrounding wildlife management areas (Mazizi-Resources-Pty-Ltd 2009). Their movements are not restricted by fences other than the veterinary cordon fences surrounding the Okavango Delta and are thus mainly dictated by water availability. During the wet season they are widely distributed throughout the wildlife management areas, while in the dry season they concentrate along the permanent rivers or move further up into the Delta (Mazizi-Resources-Pty-Ltd 2009).

1.3.1.1.1 Impacts on habitat

1.3.1.1.1.1 Vegetation

Elephants are highly destructive feeders, consuming up to 200kg of vegetation per day (Estes, 1991), and are estimated to consume only 50 % of the biomass broken off trees and shrubs during feeding (du Toit et al. 2003). They forage in several different ways, either pushing down trees or removing leaves and whole branches, however late in the dry season elephants may strip large sections of bark from tree trunks. Some plants such as *Combretum* species may continue growing after being pushed over, while others such as

Colophospermum mopane and *Sclerocarya birrea* may coppice or resprout from the broken point. Others such as some *Acacia* species are unable to resprout and thus die (du Toit et al. 2003). In addition to browse between 40 and 90% of their diet may be comprised of grass biomass, which is consumed by tearing off leaves from grass tufts or removing the whole tuft from the ground and chewing it (Owen-Smith, 1988).

In the Moremi Game Reserve and surrounding wildlife management areas elephants appear to be transforming the riverine closed canopy woodland to shrub vegetation, a favoured habitat for browsers such as, kudu and impala, and game birds. This change has however been limited to the vegetation structure, while species composition and abundance remains the same. Changes in vegetation species composition have been observed in regions impacted by both elephants and late season fires (Mazizi-Resources-Pty-Ltd 2009).

While elephants are often mainly regarded as having negative impacts on their surrounding habitat they can also have a number of positive impacts. Owing to their short gut retention time (Estes 1991) and the large distances they are able to cover in a day they function as an efficient seed dispersal mechanism depositing seed, undamaged by the digestion process, a fairly substantial distance from the parent plant (Baxter and Getz 2005). Elephants also make previously inaccessible browse available to smaller species by opening up paths into dense vegetation and creating ‘browsing hedges’ by decreasing the average height of the woody layer and keeping generally unpalatable species such as mopane, palatable through repeated browsing (Styles and Skinner 2000, Kerley et al. 2008).

1.3.1.2 Other herbivores

Intense browsing pressure by impala is believed to prevent the establishment of woody seedlings. In Lake Manyara National Park there are two separate even-aged stands of *Acacia* trees which are believed to be 27 and 34 years old (Prins and van der Jeuged 1993). These germination flushes coincide with the outbreaks of anthrax in 1984 and 1977 which killed a large proportion of the impala population. In addition to this the age of a stand of *Acacia* trees in the same region believed to date back to the 1880s coincides with the rinderpest pandemic which swept through the region during the same time period (Prins and van der Jeuged 1993).

1.3.2 Community utilization

1.3.2.1 Harvesting

Of the approximately 2 million people living in Botswana 52 % live in areas classed as urban settlements (Hannah et al. 1988). These settlements may be cities, towns or villages, however only 21 % of the

population lives in cities or towns (Hannah et al. 1988). The other 79 % either live in rural areas or in villages which often do not have supplied electricity. In these areas wood is used not only for fuel (45 %) but also for fencing and building (55 %) (Hannah et al. 1988). Of the 675 000 m^3 of wood used in Botswana per year only 15 000 m^3 comes from commercial timber concessions, the rest is collected from natural vegetation (Hannah et al. 1988). Table 1.1 provides a list of the commonly utilized plant resources in the Okavango Delta.

Table 1.1: Commonly Used Plants in the Okavango Delta

Name of Plant		Part used	Common uses
Scientific Name	Common Name		
Hyphaene petersiana	Real Fan Palm	Leaves Seed Sap	Basket weaving Making ornaments and buttons Making palm wine
Phoenix reclinata	Wild Date Palm	Leaves Inflorescence Fruit Heart of leaf crown Sap	Basket weaving Used as brooms Eaten Eaten Making palm wine
Diospyros mespiliformis	Jackel Berry	Trunk Fruit	Used to carve mekoro's Eaten
Pechuel-Loeschea leubnitziae	Wild Sage	Stems	Making fishing funnels & baskets
Terminalia serecia	Silver Terminalia	Branches	Used as mekoro poles
Combretum imberbe	Leadwood	Wood Roots Fruit	Firewood Making dye Making jewellery
Euclea divinorum	Magic Gwarri	Root-bark	Making dye for basket weaving
Berchemia discolour	Birdplum	Bark Fruit	Making dye for basket weaving Eaten
Colophospermum mopane	Mopane	Wood Mopane worms	Used as building material Eaten
Kigelia africana	Sausage Tree	Trunk	Used to carve mekoro's
Pterocarpus angolensis	Kiaat	Trunk	Used to carve mekoro's
Schlerocarya birrea	Marula	Trunk Wood Fruit Fruit Seeds	Used to carve mekoro's Used to carve pestles to crush grain Making beer Eaten Eaten
Acacia species		Wood	Firewood

Source: Adapted from Harrison (2006) and Forrester *et al* (1989).

Today there are approximately 1 500 basket weavers in and around the Okavango. The majority of the curios available within the Ngamiland area are these baskets and over 70% of the tourists to the region actively seek out these curios to purchase. As a result of this basket weaving has become a lucrative industry with the majority of the commercially sold basket curios being made in the Etsha and Gumare

regions. These regions have thus suffered a substantial decline in the density of *H. petersiana*, *E. divinorum* and *B. discolor*, the plants providing the main raw materials for basket production (Harrison 2006).

1.3.2.2 Livestock

As livestock are water-dependent, stock farming in the arid regions of Africa is heavily reliant on natural and man-made water points (de Leeuw et al. 2001). This concentration of livestock at water points results in soil trampling which decreases infiltration, increases run-off, alters vegetation structure and species composition and alters tree:grass interactions (Tolsma et al. 1987, Pietola et al. 2005) ultimatly impacting both biodiversity and carrying capacity. Zones close to water points become dominated by unpalatable herbs and annual grasses, while regions further away move from thicket into wooded savanna with a diverse understory of trampling sensitive grasses and herbs (Tolsma et al. 1987). Grazed grasslands generally have low levels of plant litter and the soil tends to have high levels of organic nitrogen and carbon, resulting from deposits of easily decomposable dung and urine. In addition to this, plants increase their root biomass as a response to grazing and in doing so stimulate soil biota to increase levels of nutrient mineralization, thus increasing nutrient supply to the grazed plants (Bardgett 2005).

1.4 OKAVANGO DELTA STATE-AND-TRANSITION MODEL

This literature review has revealed fairly extensive research into the flood-driven terrestrial vegetation within the Okavango Delta system, however research into the environmental and management factors driving the dry woodland and savanna regions is lacking. The state-and-transition model depicted in Figure 1.4 provides an overview of this research and highlights knowledge gaps. Table 1.2 provides an explanation of the transitions. The research in this thesis examines the community structure within the documented savanna and woodland states and deals with transitions 10, 12, 13, 14 and 16 (Figure 1.4).

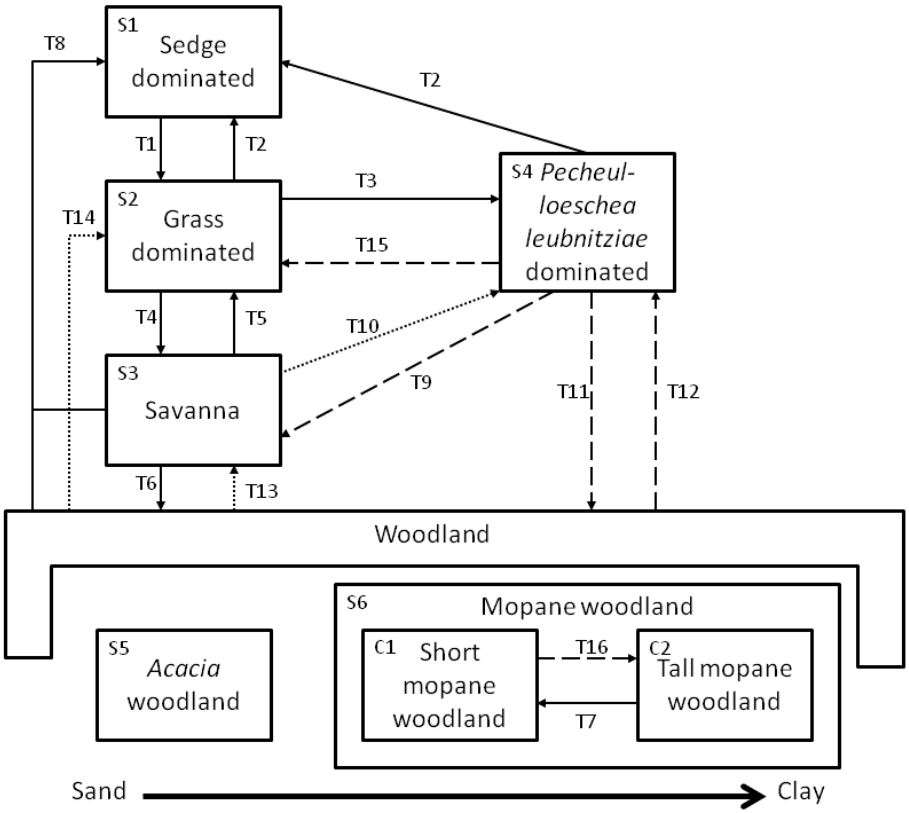

Figure 1.4: Okavango Delta terrestrial vegetation state and transition model. T indicates transitions between states. Solid lines indicate well documented transitions, dotted lines indicate transitions which may be inferred from previous research and the dashed lines indicated transitions for which no data were available.

Table 1.2: Vegetation transitions for the Okavango Delta terrestrial vegetation.

Transition	Main Causes
T1	Decrease in flooding frequency to every 2 to 5 years
T2	Annual flooding
T3	Flooding stops and area is heavily grazed/disturbed
T4	Decrease in flooding frequency to every 5 to 10 years
T5	Biennial fire, woody utilization (eg. Elephants/Wood harvesting)
T6	No flooding, infrequent burning (every 5 years+), little utilization
T7	Fire, woody utilization (eg. Elephants/Wood harvesting)
T8	Annual flooding
T9	No data
T10	Heavy utilization and disturbance
T11	No data
T12	No data
T13	Fire, woody utilization (eg. Elephants/Wood harvesting)
T14	Fire, woody utilization (eg. Elephants/Wood harvesting)
T15	No data
T16	No data

1.5 PROBLEM STATEMENT

As the population of Ngamiland grows, so the demand for natural resources and ecosystem services increases. This increasing demand intensifies the need for effective ecosystem management to ensure the sustainable use of natural resources. Integral to effective natural resource management is an understanding of the ecosystem, the composition, structure and distribution of the vegetation communities therein, and their response to various environmental and sociological drivers. The ODMP has identified two major issues to be addressed in order to allow for effective management and sustainable utilization of the Okavango Delta and the preservation of natural resources for the benefit and future well-being of the population. These issues are as follows; the influences of both human-induced and natural factors on the ecosystem, and the lack of or poor information regarding natural resources, land use factors and management of resources. While much research integral to addressing these issues has been conducted within the permanent swamp, seasonal swamp and floodplain regions of the Delta there is a paucity of knowledge regarding the species rich transition zone of dry woodland bordering these central regions.

Fire is currently not used as a management tool in the Okavango Delta and the restrictions imposed by the National Herbage Act have created a negative perception of fire. Although there is a thorough understanding of the influence of fire and the interactions between fire and flooding on the seasonal floodplains of the Okavango Delta, the influence of fire on the dry woodland and savanna regions has been largely overlooked. In addition there is little understanding of the effects different forms of livestock utilization have on these dry woodland and savanna regions and the role that shrubby pioneer species, such as *Pecheul-loeschea leubnitziae*, play in the succession of dry floodplains to savanna and woodland. As the population of Ngamiland increases, one can expect to see a concomitant increase in livestock numbers, escalating the demand for grazing resources.

1.6 PROJECT AIMS

This project was developed in order to address these deficiencies. The aims of this project are (1) to describe the composition and structure of the vegetation communities within the dry woodland and savanna vegetation the eastern Okavango Delta, (2) to map the geographic distribution of these dryland woody vegetation types in Ngamiland NG33 and NG34, (3) to develop and map morphological vegetation management units for these dry woodland and savanna communities, (4) to describe the soil characteristics underlying the morphological vegetation management units and to determine their influence on the occurrence of the dominant woody and grass species, (5) to determine the influence, in terms of species composition, density and structural composition of a single fire event on the vegetation of the vegetation management units, (6) to determine the effects in terms of species composition and

density of three different forms of vegetation utilization namely; wildlife, unrestricted community owned livestock (cattle, goats and donkeys) and restricted community owned livestock (goats and donkeys only), (7) to determine the preferred environmental conditions for the establishment of the encroaching shrub *Pecheul-loeschea leubnitziae* and (8) to determine the effect of *Pecheul-loeschea leubnitziae* on grass sward and seed bank composition.

Aims 1 to 4 examine the community structure of the documented savanna and woodland states while aim 5 provides data to explain transitions 13 and 14, aim 6 to explain transition 16 and aim 7 to explain transitions 10 and 12.

1.7 STUDY AREA

The study was conducted in the controlled hunting areas (CHA) Ngamiland NG33 and NG34 and Moremi Game Reserve (NG28) and the community areas south of the veterinary cordon fence (Figure 1.5). These dry woodland regions in the south-eastern Okavango Delta function as a transition zone between the Okavango swamps and the Kalahari Desert resulting in a region high species richness and endemism (Bourquin 2010). This area was selected as the vegetation is predominantly dry woodland and savanna and provides good representations of both *Acacia* dominated savanna and mopane dominated woodland. The proximity of the study area to the veterinary cordon fence and to Sankuyo village also afforded the opportunity for fence-line contrasts in terms of different forms of land utilization. In addition there is extensive wildlife ecology research being conducted in the area and the study will provide essential baseline data for these studies.

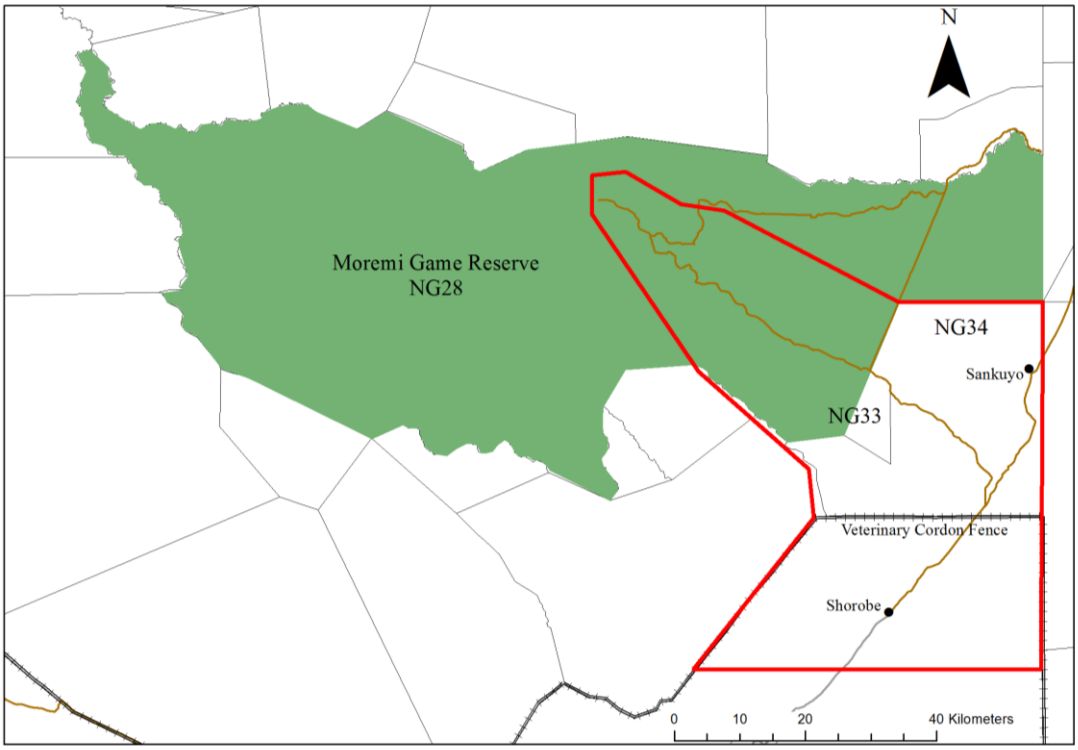

Figure 1.5: South-eastern Okavango Delta showing study area outlined in red. Tar roads are indicated in grey and dirt roads in brown.

The controlled hunting areas NG33 and NG34 are allocated to the Sankuyo Tshwarangano Management Trust and contain five tourist camps (2 hunting safari camps, 2 photographic safari camps and 1 campsite) and two research camps. Approximately 70% of the area is used for hunting and 30% for photographic tourism. NG33 and NG34 have historically been used for subsistence farming, hunting and gathering activities, as well as flood-recession farming along the Mogogelo River. Since 1996 the area has been run as a conservation area under the CBNRM program, although some veld products are still collected in the area, particularly along Mogogelo and Gomoti Rivers. Sankuyo village is the only settlement in NG33 and NG34 and has a population of approximately 400 (Mazizi-Resources-Pty-Ltd 2009, CSO 2011). The community keeps a small stock of goats and donkeys in the areas close to the village. The village of Shorobe is located south of the Veterinary Cordon Fence (Southern Buffalo Fence). The village itself has a population of approximately 1000, while the greater Shorobe area is home to an additional 2000 people (CSO 2011). The community keeps cattle, donkeys and goats.

The area experiences a dry winter season from April to September with minimum temperatures dropping to 15°C and a warm summer from October to March with maximum temperatures rising to 40°C. The

mean annual rainfall is 560mm with the majority falling between November and March (Mazizi-Resources-Pty-Ltd 2009).

The section of the study area north of the Veterinary Cordon Fence provides habitats for a wide range of mammal, reptile and bird species, many of which are rare and protected. A total of 64 mammal species have been observed in the region, 34 of which are medium to large mammal species. Of these 34 medium to large mammal species, 6 are rare or vulnerable, 2 protected by the African Convention and 4 protected by the Convention on International Trade in Endangered Species (CITES). Approximately 363 bird species are expected to occur in the area, many of which are protected by the African Convention and CITES. Sixteen bird species are known to breed in the area. Seventy-two reptile species occur in the area, one of which is classed as endangered and one of which is protected by CITES. The river systems within the area also contain approximately 55 species of fish. In addition 7 species of protected tree occur in the area, namely *Afzelia quanzensis, Guibourtia coleosperma, Pterocarpus angolensis, Entandrophragma caudatum, Adansonia digitata, Berchemia discolor* and *Diospyros mespiliformis* (Mazizi-Resources-Pty-Ltd 2009).

The extensive wildlife ecology research conducted in the area covers many of the large mammal species and several small mammal and invertebrate projects are proposed. One of these research camps in the CHA is the field base for the Botswana Predator Conservation Trust (Wild Dog Camp). The trust, founded in 1989 as a wild dog research project, conducts both predator and herbivore population monitoring. The predator population monitoring focuses on the major large carnivore species in the Okavango Delta; lion, leopard, cheetah, spotted hyena and wild dog, and documents trends in predator population size, social behaviour, habitat use, interspecies interactions and foraging patterns, while the herbivore population monitoring, conducted in the form of biennial game counts, focuses on herbivore abundance and distribution and how this affects predator distribution, prey preference and resource competition between predators (BPCT 2010). The second research camp in the area Dubatana Research Camp (HQ), run by Squacco Heron Projects Pty. Ltd. Two important post graduate studies on large herbivore species have been conducted in collaboration with the staff from this camp. The first examined the relationship between habitat availability and large herbivore population density focusing on the zebra population (Bartlam-Brookes 2010), while the second focused on the African buffalo investigating the population demographics, home range size, habitat preference, foraging patterns and triggers for large scale seasonal movements of this keystone species (Bennit 2011). In addition two more autecological studies focusing on giraffe and impala respectively have been proposed.

1.8 THESIS OUTLINE

Chapter one of this thesis provides an overview of the Okavango Delta and the vegetation communities therein and a review of the environmental and sociological factors affecting the distribution, composition and structure of those communities. In addition it provides an overview of the knowledge gaps addressed by this thesis and a description of the study area.

Chapter two addresses aims number one and two, firstly to describe the composition and structure of the vegetation communities within the dry woodland and savanna vegetation the eastern Okavango Delta and secondly to map the geographic distribution of these dryland woody vegetation types in NG33 and NG34. These aims were achieved by accomplishing the following objectives; (1) to develop a taxonomic and structurally based vegetation classification for the dry woodland and savanna regions in the eastern Okavango Delta, (2) to investigate the relationships between those vegetation types, (3) to describe those vegetation types according to the (a) species composition, in terms of abundance and frequency of occurrence, (b) mean cover (c) indicator species, (d) diversity and (e) height structure of the woody species layer and (f) species composition, in terms of abundance and frequency of occurrence, of the grass layer and (3) to develop a practical vegetation map that provides background data for the ongoing research in NG33 and NG34.

Chapter three addresses aims number three and four, firstly to develop and map morphological vegetation management units for these dry woodland and savanna communities, secondly to describe the soil characteristics underlying the morphological vegetation management units and to determine their influence on the occurrence of the dominant woody and grass species. This was done by achieving the following objectives; (1) to create a functional dry woodland and savanna vegetation classification using leaf morphology, (2) to map the geographical distribution of these vegetation management units in NG33, NG34 and Moremi Game Reserve, (3) to determine the relationship between the topsoil and subsoil characteristics underlying these vegetation management units, (4) to describe the soil characteristics underlying these vegetation management units and (5) to determine the effect of those soil characteristics on the occurrence of dominant woody and herbaceous species.

Chapter four addresses aim number five, to determine the influence, in terms of species composition, density and structural composition, of a single fire event on the vegetation of the vegetation management units, by achieving the following objectives; (1) to identify regions affected by fire in October 2008 by mapping the fire distribution from 2003 to 2009 and (2) to determine the influence of a single, widespread

fire event on the vegetation characteristics of the four vegetation management units defined in chapter three, tall mopane woodland, shrub mopane woodland, mixed broadleaf woodland and mixed thornveld.

Chapter five addresses aim number six, to determine the effects in terms of species composition and density of three different forms of vegetation utilization namely; wildlife, unrestricted community owned livestock (cattle, goats and donkeys) and restricted community owned livestock (goats and donkeys only). The objective of this chapter was to determine the effects of the three different forms of vegetation utilization on; (1) the woody layer composition and structure and (2) the grass composition and cover in shrub mopane woodland and mixed thornveld.

Chapter six addresses aim number seven, to determine the effect of *Pecheul-Loeschea leubnitziae* on grass sward and seed bank composition. The objective of this chapter was to determine the following; (1) the correlation between seedbank and aboveground vegetation characteristics (2) the influence of above ground cover of *Pecheul-Loeschea leubnitziae* on relative abundance of grass species within the seedbank, (3) the effect of *Pecheul-Loeschea leubnitziae* above ground cover on species composition of above ground vegetation and (4) the influence of aboveground of *Pecheul-Loeschea leubnitziae* cover on relative proportions of grasses and non-grass species within a seed bank.

Chapter seven addresses aim number eight, to determine the preferred environmental conditions for the establishment of the encroaching shrub *Pecheul-Loeschea leubnitziae.* The objective of this chapter was to determine the environmental drivers affecting the occurrence of *P. leubnitziae*.

Chapter eight presents a synthesis of the findings of the study and how they relate to and augment the current understanding of the vegetation of the Okavango Delta.

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CHAPTER 2 : CLASSIFICATION AND MAPPING OF THE DRY WOODLAND AND SAVANNA IN THE EASTERN OKAVANGO DELTA

2.1 INTRODUCTION

De Cáceres and Wiser (2011) state that 'Vegetation classification is a useful tool for basic and applied research as well as for environmental management'. The major goal when conducting such an exercise is to simplify a complex continuous system in order to; understand how species are distributed and why, understand how both individual species and species assemblages affect the ecosystem and to predict how species, communities and landscapes will respond to environmental changes (Symstad 2002). As a result of the varied applications of vegetation classification the properties utilized in their construction are equally varied (Symstad 2002, De Cáceres and Wiser 2011). The more commonly used properties as listed by Symstad (2002) are; structure, taxonomy, resource use, response to change and role in ecosystem function.

Structurally based vegetation classifications are the oldest and most simple form, utilizing growth form to produce groupings such as trees, shrubs and grasses. These classifications have limited applicability and are often included in other more detailed classifications to provide additional data. Taxonomically based classification systems provide a detailed description of community composition, however they should be used in conjunction with structural classification, as populations of similar species may differ morphologically due to environmental conditions (Symstad 2002). Resource use is a more complex property to define as it requires the inclusion of both the method of resource use, as well as type of resource utilized. This form of classification is usually used to describe feeding guilds. Classifications which produce functional types or response groups are more commonly used in environmental management, as they increase understanding of how the vegetation interacts with the environment. Possibly the most complex classifications to produce are those using specific species role in ecosystem function. While these classifications provide useful insight into the functional effect groups within a system, they require extensive background data to produce (Symstad 2002). Vegetation classification becomes an even more powerful research and management tool when combined with some form of mapping indicating the distribution of the groupings produced.

The current trends in vegetation mapping are strongly influenced by the availability of remote sensing tools (Bredenkamp et al. 1998). Over reliance on these remote sensing tools may result in map inaccuracies. Both poor resolution of the available predictor variable maps and low levels of correlation

between predictor variables and vegetation units may affect map accuracy (Van Etten 1998). These remote sensing techniques may however be an extremely powerful tool if used in conjunction with the appropriate field studies (Bredenkamp et al. 1998). One of the more efficient methods for the construction of multi-use vegetation maps is a floristic based classification, supported by multivariate analysis and structural data (Dias et al. 2004). This allows the classification to be used to investigate both long-term processes indicated by the floristic composition and short-term processes indicated by the structural composition (Lux and Bemmerlein-Lux 1998). This allows the maps to be utilized for a range of purposes such as; landscape planning, development and implementation of management plans, forestry, conservation, monitoring and many varied forms of research (Bredenkamp et al. 1998, Dias et al. 2004).

Although a vegetation map covering the whole of Ngamiland (110 000 km^2) was produced in 2002 using landsat images, aerial photographs and 502 vegetation transects (Jellema et al. 2002), it has limited applicability to research within the Okavango Delta as the Delta itself only comprises 26% of the mapped area (Ramberg et al. 2006) severely limiting the mapping accuracy at a fine scale. Examination of the literature concerning vegetation classification in the Okavango Delta, revealed several other studies focussed on the peripheral dryland regions of the Okavango Delta (Tinley 1966, Rűbbel and Child 1976, Ringrose et al. 2003, McCarthy et al. 2005) which refer specifically to different types of woody cover at a finer scale than the broad division of *Acacia* dominated woodland and tall and short *Colophospermum mopane* dominated woodlands (Ellery and Ellery 1997). However the scope of these studies was restricted to specific objectives, limiting future use of the classifications developed. Two of the studies focused on the use of satellite imagery; with one monitoring ecological changes (Ringrose et al. 2003) and the other investigating the potential for mapping ecoregions at a Delta-wide scale (McCarthy et al. 2005). The other two focused on the description of the vegetation in Moremi Game Reserve; with one describing eight woody communities (Tinley 1966) and the other investigating the level of bush encroachment in five woody communities (Rűbbel and Child 1976). The studies focusing on the use of satellite imagery made little reference to woody cover percentages and structural composition. Only Tinley (1966) and Ringrose et al. (2003) provide suitably detailed descriptions of the floristic composition of the vegetation types discussed and none of these studies provide a map of the vegetation types. Within these four vegetation studies there is great variation in the number of woody vegetation classes described. Tinley (1966) describes eight, while Rübbel and Child (1976) describe five. Ringrose et al. (2003) describe twelve ecological units in total of which seven are woody dominated, while McCarthy et al. (2005) describe only four. This variation is largely due to the objectives of each study, although some may be attributed to methodology and study area. Ringrose et al. (2003) conducted their field surveys in the Xudum region of the south-western Okavango Delta, while Tinley (1966) worked in Moremi Game

Reserve. Ringrose et al. (2003) does however provide a slightly more detailed description of the species composition within the *Colophospermum mopane* dominated vegetation types, describing three distinct groups, while Tinley (1966) describes only two forms of *C. mopane* woodland focusing on structural composition. As the vegetation classifications produced by these studies were highly variable and biased towards the objectives of each particular study or study area it is difficult to utilize them for further research and management purposes. For this reason this study sought to develop an objective vegetation classification accompanied by a detailed description.

The objectives of this study were to (1) develop a taxonomic and structurally based vegetation classification for the dry woodland and savanna regions in the eastern Okavango Delta, (2) investigate the relationships between those vegetation types, (3) provide a detailed description of those vegetation types according to the (a) species composition, in terms of abundance and frequency of occurrence, (b) mean cover (c) indicator species, (d) diversity and (e) height structure of the woody species layer and (f) species composition, in terms of abundance and frequency of occurrence, of the grass layer and (3) develop a practical vegetation map that provides background data for the ongoing research in NG33 and NG34.

2.2 METHODS

2.2.1 Data collection

The composition and structure of the dryland woody dominated vegetation in NG33 and NG34 was sampled using two hundred and fifty-six (50m by 50m) plots, stratified to cover the study area as extensively as possibly, sampled between February and May 2009. Plot locations were selected to cover the study area as extensively as possible with the minimum distance between any two sites being one kilometre (Figure 2.1).

At each sample plot all woody species were recorded and each species was allocated a cover abundance value in a similar style to that used in the Braun-Blanquet method (Mueller-Dombois and Ellenberg 1974) but using absolute cover values rather than ranking species according to a scale. In addition the total woody cover was visually estimated and GPS co-ordinates were recorded for each plot. The structural composition of the woody layer was sampled by visually estimating the relative cover of each of the following height classes, <0.5m, 0.5-0.99m, 1-1.99m, 2-2.99m and >3m. To allow for a complete description of the vegetation to be developed, the proportional species composition of the grass sward in each plot was also estimated.

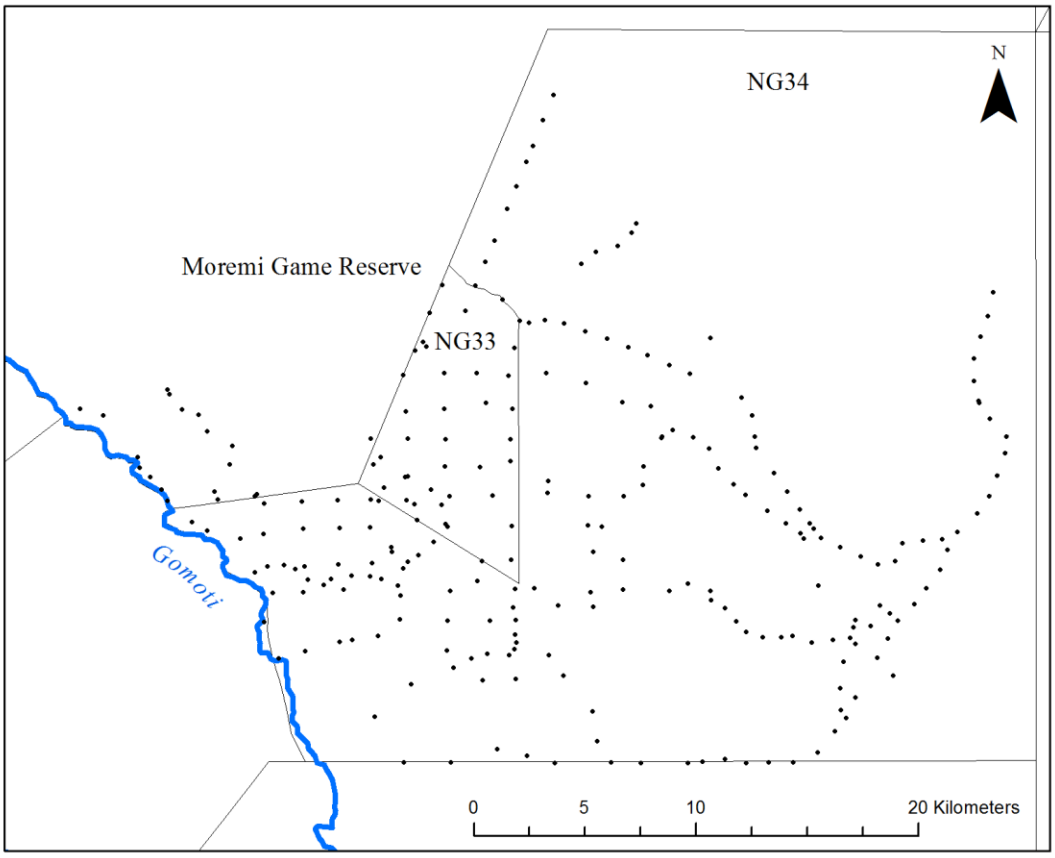

Figure 2.1: Sample sites used for vegetation mapping in NG33, NG34 and Moremi Game Reserve.

2.2.2 Data Analysis

2.2.2.1 Vegetation classification

The woody species absolute cover data were subjected to an agglomerative, hierarchical cluster analysis (ACL) (in the software program PRIMER (Clarke and Gorley 2006)) using the group mean and Bray-Curtis similarity to create groups. A similarity profile test (SIMPROF) conducted in the software program PRIMER (Clarke and Gorley 2006) was used to calculate the significance level at each node of the dendrogram and to indentify significantly different groups or vegetation types.

2.2.2.2 Relationships between vegetation types

The relationships between groups were then displayed using non-metric multidimensional scaling (NMS) in WINKYST (Smilauer 2002) and then rotated using a principle components analysis (PCA) in CANOCO (ter Braak and Smilauer 1997).

2.2.2.3 Vegetation type description

2.2.2.3.1 Woody layer

2.2.2.3.1.1 Species composition

Mean abundance and frequency of occurrence data for each woody species were calculated for each vegetation type. In addition mean woody cover and maximum and mean species richness was calculated for each vegetation type. Vegetation classes with a mean woody cover of greater than 50% were considered to be closed canopy and those with a mean woody cover of less than 50% were considered to be open canopy.

2.2.2.3.1.2 Indicator species

An indicator species analysis was conducted in PC-ORD (McCune and Mefford 1997) to identify indicator species and their percentage contribution to the woody species composition for the vegetation types identified by the cluster analysis, using 10 000 permutations in a Monte Carlo test (McCune and Mefford 1997).

2.2.2.3.1.3 Diversity indices

Diversity within the vegetation types was described using mean Hill's diversity indices and mean Pielou's evenness co-efficient (Begon et al. 2005) using the following followingb formulae:

Hill's N1 = $e^{H'}$, where $H' = -\Sigma p_i.\ln(p_i)$ and p_i = the proportion of species i in the sample

Hill's N2 = $1/\lambda$, where $\lambda = \Sigma n_i(n_i - 1)/N(N-1)$

n_i = number of individuals of species i in the sample

N = total number of individuals in the sample

Pielou's evenness co-efficient = $H'/\ln S$, where S = total number of species in the sample

Hill's diversity indices N1 and N2 describe the diversity of abundant and very abundant species respectively, while Pielou's evenness co-efficient compliments the diversity indices with values ranging from 0 to 1 and low values indicating that the species composition is dominated by certain species (Begon et al. 2005).

2.2.2.3.1.4 Height structure

Differences in height structure between the groups were examined using an analysis of similarity (ANOSIM) in PRIMER using Bray-Curtis similarity and 9999 permutations (Clarke and Gorley 2006). The p-values were controlled for false discovery rate using the Benjamani and Hochberg procedure

(Verhoeven et al. 2005). A similarity percentages routine (SIMPER) also conducted in PRIMER (Clarke and Gorley 2006) was then used to determine the contribution of each height class to the average Bray-Curtis similarity between groups. The structure of the groups was displayed using a variable width stacked histogram developed in SigmaPlot (SigmaPlot 2002) and relationships between the groups were displayed graphically using a correspondence analysis (CA) in CANOCO (ter Braak and Smilauer 1997). Vegetation was considered to be tall if more than 35% of the woody layer fell into the height class >3m, while it was considered to be short if less than 30% of the woody component fell into this height class.

2.2.2.3.2 Grass layer

2.2.2.3.2.1 Species composition

Mean abundance and frequency of occurrence data for each grass species were calculated for each vegetation type.

2.2.2.4 Mapping

Sites were mapped using ArcMap 10 (ESRI 2010) and categorised according to vegetation type. The distribution of these points was overlaid on aerial photographs obtained from the Okavango Research Institute (ORI) and the geographical extent of the vegetation types was mapped.

2.3 RESULTS

2.3.2 Vegetation Classification

The agglomerative cluster analysis and SIMPROF test produced 18 groups, which were significantly different from one another at a 5% level, with eight groups on the left of the dendrogram and ten on the right. Of the eight groups on the right of the dendrogram, seven were dominated by *Colophospermum mopane*, while the eighth (Group A) (Figure 2.2) had less than 5% woody species cover. Owing to the fact that the focus of the classification was the woody dominated vegetation types and that only two of the 265 sites sampled fell into this group the sites were regarded as outliers and the group was removed from the dataset and further analyses. The seven remaining groups on the left of the dendrogram were examined in terms of between group similarity and as *Colophospermum mopane* dominated woodland tends to be fairly uniform (Mendelsohn et al. 2010) those groups with a similarity of greater than 70% were combined. The total woody cover, percentage cover of *C. mopane* and the species richness of the groups was also examined to confirm similarity before they were combined. The species composition of the ten groups on the right of the dendrogram was more variable and therefore only those groups which were dominated by *Acacia erioloba* and had a similarity of greater than 40% were combined. The total

woody cover and species richness of these groups was also examined before combining groups in order to confirm similarity. This resulted in the final 11 groups (Figure 2.2).

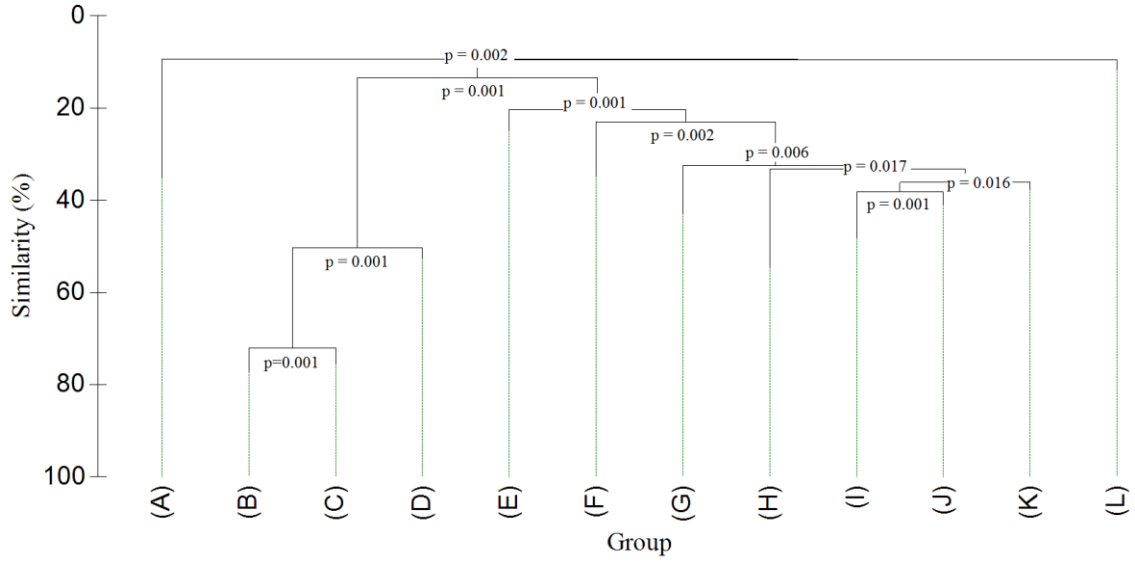

Figure 2.2: Compressed cluster analysis of absolute cover of woody species showing p-values indicating differences between groups.

The vegetation types derived from this classification are as follows; Group B - Tall pure mopane woodland, Group C - Tall mixed mopane woodland, Group D - Short mixed mopane woodland, Group E - Short mixed broadleaf woodland, Group F - Open mixed *Acacia* veld, Group G - Closed *Acacia-Combretum* woodland, Group H - Closed mixed *Acacia* veld, Group I - Closed *Acacia erioloba* savanna, Group J - Tall mixed broadleaf woodland, Group K - Open *Acacia erioloba* savanna and Group L - Palm thornveld (Figure 2.2).

2.3.3 Relationship between vegetation types

Colophospermum mopane dominated groups, tall pure mopane woodland, tall mixed mopane woodland and short mixed mopane woodland were located close to one another in ordination space on the left of axis one. The sites in tall pure mopane woodland and tall mixed mopane woodland formed tight clusters, while the spread of sites in short mixed mopane woodland was slightly broader, indicating a more species diverse *C. mopane* dominated class. Palm thornveld had an extremely broad spread of sites overlapping all groups except the three *C. mopane* dominated groups, tall pure mopane woodland, tall mixed mopane woodland and short mixed mopane woodland. Closed mixed *Acacia* veld was a very small group comprising only 2 sites and fell entirely within open mixed *Acacia* veld. Open mixed *Acacia* veld in turn

fell almost entirely within palm thornveld. Closed *Acacia-Combretum* woodland, closed *Acacia erioloba* savanna, tall mixed broadleaf woodland and open *Acacia erioloba* savanna were closely clustered to the right of the centroid along axis one (Figure 2.3) and overlapped substantially. Closed *Acacia erioloba* savanna and tall mixed broadleaf woodland overlapped by approximately half, and closed *Acacia-Combretum* woodland, containing only 3 sites, overlapped substantially with both these groups. Short mixed broadleaf woodland had the second widest spread of sites of all eleven groups and overlapped by approximately half with palm thornveld. It fell between the *C. mopane* dominated groups, tall pure mopane woodland, tall mixed mopane woodland and short mixed mopane woodland, and Open mixed *Acacia* veld and palm thornveld (Figure 2.3).

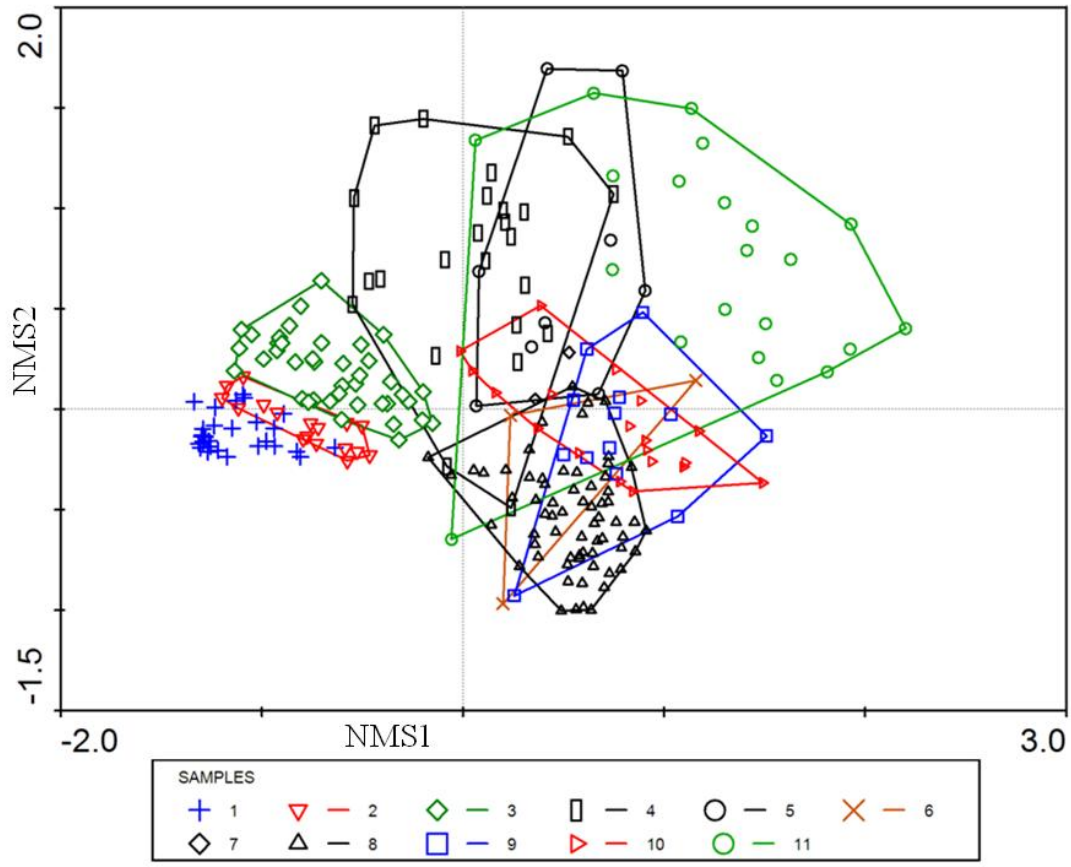

Figure 2.3: Non-metric multidimensional scaling (NMS) of species composition rotated using principle components analysis (PCA) showing 11 groups produced by ACL. Eigenvalues of axes one and two are 0.719 and 0.281, representing a cumulative variance of 100%. 1 = Tall pure mopane woodland, 2 = Tall mixed mopane woodland, 3 = Short mixed mopane woodland, 4 = Short mixed broadleaf woodland, 5 = Open mixed *Acacia* veld, 6 = Closed *Acacia-Combretum* woodland, 7 = Closed mixed *Acacia* veld, 8 = Closed *Acacia erioloba* savanna, 9 = Tall mixed broadleaf woodland, 10 = Open *Acacia erioloba* savanna, 11 = Palm thornveld.

2.3.4 Vegetation type description

2.3.4.1 Woody layer

2.3.4.1.1 Species composition and indicator species

Palm thornveld has a mean cover of 36% (± 4.3) and is dominated by *Ziziphus mucronata* and *Hyphaene petersiana* (Table 2.1). These two species occur in 52% and 57% of the sites in this group and have mean abundances of 8% (± 2.6) and 7% (± 2.1) respectively (Table 2.1). Indicator species analysis identified *Hyphaene petersiana* as an indicator species for this group with an indicator value of 37 ($p = 0.017$) (Table 2.3). Palm thornveld has variable species richness with a mean of 4.9 (± 0.34) and a maximum of 7.0 (Table 2.1)

The second major division at approximately 15% similarity divides the groups according to the dominance of *Colophospermum mopane* with one grouping comprised of tall pure mopane woodland, tall mixed mopane woodland and short mixed mopane woodland and the other of short mixed broadleaf woodland, open mixed *Acacia* veld, closed *Acacia-Combretum* woodland, closed mixed *Acacia* veld, closed *Acacia erioloba* savanna, tall mixed broadleaf woodland, and open *Acacia erioloba* savanna. Short mixed mopane woodland separates from the rest of the grouping at approximately 50% similarity, while tall pure mopane woodland and tall mixed mopane woodland separate at just over 70% similarity (Figure 2.2).

Tall pure mopane woodland had the highest mean woody cover of the groups with a value of 92% (± 0.9) (Table 2.1). *C. mopane* was the most dominant species; occurring in all 45 sites in the group (Table 2.2) and accounting for 86% (± 1.2) of the woody cover (Table 2.1). It was a significant indicator for this group with an indicator value of 42 ($p < 0.001$) (Table 2.3). The species richness of this group was fairly low with a mean value of 1.9 (± 0.14) and a maximum of 4.0 (Table 2.1).

Tall mixed mopane woodland was also dominated by *C. mopane,* occurring in all 18 sites in this group (Table 2.2), but the species only contributed 59% (± 1.9) of the total 75% (± 3.4) woody cover (Table 2.1). *Acacia erioloba* was also a fairly dominant species in this group, occurring in 67% of the sites (Table 2.2) and contributing 7% (± 1.6) of the total woody cover (Table 2.1). As seen in tall pure mopane woodland, *C. mopane* was found to be a significant indicator species for this group with an indicator value of 29 ($p < 0.001$) (Table 2.3). Tall mixed mopane woodland had a slightly higher species richness than tall pure mopane woodland, with a mean species richness of 3.3 (± 0.32) and a maximum of 5.0 (Table 2.1).

Short mixed mopane woodland had a total woody cover of 66% (± 3.1) with 34% (±1.3) of this cover contributed by *C. mopane* and 6% (± 0.9) by *A. erioloba* (Table 2.1). *Acacia erioloba* occurred in 68% of the sites, while *C. mopane* was recorded in all 41 sites in this group (Table 2.2). As in tall pure mopane woodland and tall mixed mopane woodland, *C. mopane* was found to be a significant indicator for this group with an indicator value of 17 ($p < 0.001$) (Table 2.3). The species richness of this group was the most variable of the three *C. mopane* dominated groups with a mean species richness of 5.2 (± 0.32) and a maximum of 11.0 (Table 2.1).

Short mixed broadleaf woodland comprises of 24 sites (Table 2.4) separated at 20% similarity (Figure 2.2). The 66% (± 3.2) woody cover (Table 2.1) observed in this group is dominated by *A. erioloba* (9% ± 1.6), *Lonchocarpus nelsii* (15% ± 2.8) and *Terminalia sericea* (19% ± 3.0) (Table 2.1). Both *L. nelsii* and *T. sericea* were found to be indicator species for this group with indicator values of 30 ($p = 0.034$) and 55 ($p = 0.003$) respectively (Table 2.4). In addition *Dichrostachys cinerea* had a significant indicator species value of 31 ($p = 0.030$) (Table 2.4) despite the species cover being only 8% (± 2.6) (Table 2.1). The mean species richness for this group was 5.0 (± 0.30) while the maximum was 8.0 (Table 2.4).

Open mixed *Acacia* veld then separated at approximately 25% similarity (Figure 2.2) and has a mean woody cover of 41% (± 4.9) (Table 2.1). This site is dominated by three *Acacia* species; *A. erioloba* (7% ± 1.5), *Acacia hebeclada* (16% ± 2.7) and *Acacia luederitzii* (8% ± 2.6) (Table 2.1) which occur in 78%, 100% and 78% of the 9 sites in this group respectively (Table 2.2). *A. hebeclada* and *A. luederitzii* were found to be indicator species for this group with indicator values of 56 ($p = 0.001$) and 44 ($p = 0.009$) (Table 2.3). Closed mixed *Acacia* veld has similar species richness to short mixed broadleaf woodland with a mean of 5 (± 0.6) and a maximum of 8.0 (Table 2.1).

Closed *Acacia-Combretum* woodland and closed mixed *Acacia* veld separated at just over 30% similarity (Figure 2.2), with closed *Acacia-Combretum* woodland having 3 sites and closed mixed *Acacia* veld having 2 sites (Table 2.4). These two groups have a mean woody cover of 67% (± 14.5) and 73% (± 22.5) respectively (Table 2.1). They are both dominated by *A. erioloba* which occurs in 100% of the sites in both groups (Table 2.2) with a mean cover of 13% (± 2.6) in closed *Acacia-Combretum* woodland and 17% (± 2.0) in closed mixed *Acacia* veld (Table 2.1). *Combretum imberbe* was also dominant in closed *Acacia-Combretum* woodland (25% ± 8.4) while *Acacia nigrescens* was also dominant in closed mixed *Acacia* veld (34% ± 18.6) (Table 2.1). *Combretum imberbe* was found to be an indicator for closed *Acacia-Combretum* woodland with an indicator value of 61 ($p = 0.001$), while *A. nigrescens*, *Acacia hebeclada* and *Boscia albitrunca* were indicator species for closed mixed *Acacia* veld with indicator

values of 90 ($p < 0.001$), 50 ($p = 0.009$) and 38 ($p = 0.013$) respectively (Table 2.3). Both *A. hebeclada* and *B. albitrunca* have a cover of less than 5% in closed mixed *Acacia* veld (Table 2.1). The species richness of the two groups was similar with closed *Acacia-Combretum* woodland having a mean species richness of 5.7 (± 0.33) and a maximum of 6.0 and closed mixed *Acacia* veld having a mean species richness of 7.0 (±1.00) and a maximum of 8.0 (Table 2.1).

Closed *Acacia erioloba* savanna, tall mixed broadleaf woodland and open *Acacia erioloba* savanna separate at a similarity of approximately 35% (Figure 2.2). Open *Acacia erioloba* savanna has a mean woody cover of 23% (± 12.7) (Table 2.1) and is dominated by *A. erioloba,* which occurs in all of the 19 sites in the group (Table 2.2) with a mean cover of 12% (± 0.7) (Table 2.1). The indicator species for this group was *A. erioloba* with an indicator value of 9 ($p = 0.009$) (Table 2.3). The species richness in closed *Acacia erioloba* savanna is variable with a mean of 4.4 (± 1.98) and a maximum of 8.0 (Table 2.1). Closed *Acacia erioloba* savanna and tall mixed broadleaf woodland had a mean woody cover of 50% (± 1.8) and 66% (± 4.5) respectively and are both dominated by *A. erioloba* with a mean abundance of 32% (±1.5) in closed *Acacia erioloba* savanna and 17% (±1.8) in tall mixed broadleaf woodland (Table 2.1). Tall mixed broadleaf woodland is also dominated by *Croton megalobotrys* (21% ± 2.4) (Table 2.1). These species occurred in all 68 sites in closed *Acacia erioloba* savanna and 13 sites in tall mixed broadleaf woodland (Table 2.2). *Acacia erioloba* was an indicator species for closed *Acacia erioloba* savanna with an indicator value of 26 ($p = 0.009$), while *C. megalobotrys* was an indicator for tall mixed broadleaf woodland with an indicator value of 65 ($p < 0.001$) (Table 2.3). The mean species richness for closed *Acacia erioloba* savanna was 4.2 (± 0.24) and for tall mixed broadleaf woodland was 5.9 (± 0.64), while the maximum species richness for the two groups were 8.0 and 10.0 respectively (Table 2.1).

Table 2.1: Mean abundance (%) (±SE) of woody species, mean species richness (SR), maximum species richness and maximum woody cover (%) in the vegetation types of NG33 and NG34. Species abbreviations are explained in Appendix A

	Tall pure mopane woodland	Tall mixed mopane woodland	Short mixed mopane woodland	Short mixed broadleaf woodland	Open mixed *Acacia* veld	Closed *Acacia-Combretum* woodland	Closed mixed *Acacia* veld	Closed *Acacia erioloba* savanna	Tall mixed broadleaf woodland	Open *Acacia erioloba* savanna	Palm thornveld
ADI	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0
AER	1 ± 0.5	7 ± 1.6	6 ± 0.9	9 ± 1.6	7 ± 1.5	13 ± 2.6	17 ± 2.0	3 ± 1.5	17 ± 1.8	12 ± 0.7	3 ± 0.9
AHE	0 ± 0.0	1 ± 0.6	2 ± 0.5	2 ± 0.9	16 ± 2.7	4 ± 2.0	0 ± 0.0	2 ± 0.5	0 ± 0.0	1 ± 0.2	2 ± 0.8
ALU	0 ± 0.0	1 ± 0.6	1 ± 0.8	2 ± 0.9	7 ± 2.6	0 ± 0.0	0 ± 0.0	1 ± 0.3	1 ± 0.5	0 ± 0.0	0 ± 0.0
AME	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0
ANI	0 ± 0.0	0 ± 0.0	0 ± 0.0	1 ± 0.4	0 ± 0.0	0 ± 0.0	34 ± 18.6	1 ± 0.2	0 ± 0.0	0 ± 0.0	2 ± 0.7
ASI	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0
AHA	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	1 ± 1.3	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0
BAL	0 ± 0.0	2 ± 0.6	3 ± 0.6	2 ± 0.6	0 ± 0.0	0 ± 0.0	5 ± 0.1	0 ± 0.0	0 ± 0.0	1 ± 0.3	0 ± 0.0
BMO	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	1 ± 0.0	1 ± 1.2	1 ± 1.3	0 ± 0.0	1 ± 1.0	0 ± 0.0	0 ± 0.0
CMO	86 ± 1.2	59 ± 1.9	34 ± 1.3	6 ± 1.5	4 ± 1.4	4 ± 2.3	5 ± 0.1	2 ± 0.6	2 ± 0.5	2 ± 0.9	1 ± 0.6
CHE	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0
CIM	0 ± 0.0	1 ± 0.8	1 ± 0.3	0 ± 0.0	1 ± 0.7	25 ± 8.4	0 ± 0.0	3 ± 0.7	7 ± 2.7	1 ± 0.3	2 ± 0.6
CMZ	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0
CME	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	2 ± 1.2	2 ± 1.3	0 ± 0.0	0 ± 0.0	21 ± 2.4	1 ± 0.3	4 ± 1.3
DCI	0 ± 0.0	0 ± 0.0	1 ± 0.3	8 ± 2.6	1 ± 0.8	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	1 ± 0.8	0 ± 0.0
DLY	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	1 ± 0.7	0 ± 0.0	3 ± 1.3
DME	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0
GFA	1 ± 0.3	0 ± 0.0	1 ± 0.4	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0
GFS	1 ± 0.2	0 ± 0.0	1 ± 0.4	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	1 ± 0.1	1 ± 0.5	1 ± 0.8	0 ± 0.0
GRE	1 ± 0.6	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0
GSE	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	2 ± 1.5	0 ± 0.0	0 ± 0.0	2 ± 1.5	0 ± 0.0	0 ± 0.0
HPE	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	1 ± 1.2	1 ± 1.3	0 ± 0.0	1 ± 0.3	1 ± 0.3	7 ± 2.1
KAF	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.2	0 ± 0.0	0 ± 0.0
LCA	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	1 ± 1.2	0 ± 0.0	0 ± 0.0
LNE	1 ± 0.3	1 ± 0.3	6 ± 1.1	15 ± 2.8	2 ± 0.8	0 ± 0.0	2 ± 2.4	2 ± 0.5	6 ± 1.8	2 ± 0.6	2 ± 0.9
RTE	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	14 ± 13.5	0 ± 0.0	0 ± 0.0	2 ± 1.1	0 ± 0.0	0 ± 0.0
TSE	0 ± 0.0	1 ± 0.7	3 ± 1.1	19 ± 3.0	0 ± 0.0	0 ± 0.0	1 ± 1.3	0 ± 0.0	0 ± 0.0	2 ± 0.7	0 ± 0.0
XAM	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	1 ± 0.4	0 ± 0.0	0 ± 0.0
ZMU	0 ± 0.0	1 ± 0.4	1 ± 0.2	1 ± 0.3	0 ± 0.0	1 ± 1.2	5 ± 4.8	2 ± 0.5	3 ± 1.2	1 ± 0.2	8 ± 2.6
UNK	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0
Mean SR	1.9 ± 0.14	3.3 ± 0.32	5.2 ± 0.32	5.0 ± 0.30	5.2 ± 0.57	5.7 ± 0.33	7.0 ± 1.00	4.2 ± 0.24	5.9 ± 0.64	4.4 ± 1.98	4.4 ± 0.34
Max SR	4.0	5.0	11.0	8.0	8.0	6.0	8.0	8.0	10.0	8.0	7.0
Mean cover	92 ± 0.9	75 ± 3.4	66 ± 3.1	66 ± 3.2	41 ± 4.9	67 ± 14.5	73 ± 22.5	50 ± 1.8	66 ± 4.5	23 ± 12.7	36 ± 4.3

Table 2.2: Frequency (%) of woody species in the vegetation types of NG33 and NG34. Species abbreviations are explained in Appendix A

	Tall pure mopane woodland	Tall mixed mopane woodland	Short mixed mopane woodland	Short mixed broadleaf woodland	Open mixed *Acacia* veld	Closed *Acacia-Combretum* woodland	Closed mixed *Acacia* veld	Closed *Acacia erioloba* savanna	Tall mixed broadleaf woodland	Open *Acacia erioloba* savanna	Palm thornveld
AER	18	67	68	88	78	100	100	100	100	100	52
AHE	0	17	24	21	100	67	0	28	0	26	24
ALU	4	17	7	25	78	0	0	16	8	5	5
AME	0	0	0	0	0	0	0	1	8	0	0
ANI	0	0	0	8	0	0	100	9	8	11	43
ASI	0	0	0	0	0	0	0	0	8	0	0
AHA	0	0	0	0	0	0	50	0	0	0	0
BAL	2	39	46	42	11	0	100	10	0	21	0
BMO	2	0	0	4	44	33	50	3	8	11	5
CMO	100	100	100	58	56	67	100	34	46	37	10
CHE	0	0	5	4	0	0	0	6	8	0	0
CIM	4	17	17	4	22	100	0	46	62	26	29
CMZ	2	6	2	4	0	0	0	0	0	5	0
CME	0	6	2	4	22	67	0	26	100	21	43
DCI	4	0	7	42	11	0	0	3	0	11	0
DLY	2	6	0	0	22	0	0	6	15	5	24
GFA	11	0	5	0	0	0	0	6	8	5	0
GFS	11	6	20	8	0	0	0	15	15	16	5
GRE	16	0	0	0	0	0	0	0	0	0	0
GSE	0	6	2	4	11	33	0	7	23	11	5
HPE	0	0	0	8	11	33	50	9	23	26	57
KAF	0	0	0	0	0	0	0	0	8	0	10
LCA	0	0	2	4	0	0	0	4	8	11	14
LNE	13	11	59	75	33	0	50	25	54	32	43
RTE	0	0	2	0	0	33	0	12	23	5	5
TSE	0	22	37	79	0	0	50	12	0	26	0
XAM	0	0	0	4	11	0	0	0	15	5	0
ZMU	0	17	12	13	11	33	50	46	38	26	52
UNK	0	0	0	4	0	0	0	0	0	0	0
DME	0	0	0	0	0	0	0	0	8	0	5
ADI	0	0	0	0	0	0	0	0	0	0	10

Table 2.3: Indicator values of species for the vegetation types of NG33 and NG34. Indicators for each group are shaded and maximum values for each species in bold. * denotes a significant value. Species abbreviations are explained in Appendix A

	Tall pure mopane woodland	Tall mixed mopane woodland	Short mixed mopane woodland	Short mixed broadleaf woodland	Open mixed *Acacia* veld	Closed *Acacia-Combretum* woodland	Closed mixed *Acacia* veld	Closed *Acacia erioloba* savanna	Tall mixed broadleaf woodland	Open *Acacia erioloba* savanna	Palm thornveld	p-value
ADI	0	0	0	0	0	0	0	0	0	0	**10**	0.089
AER	0	4	3	6	4	10	14	**26**	14	9	1	0.009*
AHE	0	1	2	1	**56**	9	0	2	0	0	1	0.001*
ALU	0	1	1	4	**44**	0	0	1	0	0	0	0.009*
AME	0	0	0	0	0	0	0	0	**6**	0	0	0.179
ANI	0	0	0	0	0	0	**90**	0	0	0	3	<0.001*
ASI	0	0	0	0	0	0	0	0	**8**	0	0	0.101
AHA	0	0	0	0	0	0	**50**	0	0	0	0	0.009*
BAL	0	6	10	7	0	0	**38**	0	0	1	0	0.013*
BMO	0	0	0	0	7	7	**11**	0	1	1	0	0.199
CMO	**42**	29	17	2	1	1	2	0	0	0	0	<0.001*
CHE	0	0	1	1	0	0	0	**2**	**2**	0	0	0.862
CIM	0	0	0	0	1	**61**	0	4	10	0	1	0.001*
CMZ	0	**2**	0	1	0	0	0	0	0	0	0	0.870
CME	0	0	0	0	1	5	0	1	**65**	0	6	<0.001*
DCI	0	0	0	**31**	1	0	0	0	0	1	0	0.030*
DLY	0	0	0	0	2	0	0	0	4	0	**13**	0.179
DME	0	0	0	0	0	0	0	0	**5**	0	2	0.253
GFA	**4**	0	1	0	0	0	0	1	2	0	0	0.567
GFS	1	0	**4**	1	0	0	0	1	2	**4**	0	0.849
GRE	**16**	0	0	0	0	0	0	0	0	0	0	0.113
GSE	0	0	0	0	0	10	0	0	**11**	1	0	0.226
HPE	0	0	0	0	0	3	5	0	1	1	**37**	0.017*
KAF	0	0	0	0	0	0	0	0	2	0	**7**	0.185
LCA	0	0	0	0	0	0	0	0	**4**	1	**4**	0.595
LNE	0	0	9	**30**	1	0	3	1	8	1	3	0.034*
RTE	0	0	0	0	0	**28**	0	0	2	0	0	0.038
TSE	0	1	5	**55**	0	0	2	0	0	1	0	0.003*
XAM	0	0	0	1	1	0	0	0	**10**	0	0	0.114
ZMU	0	1	0	0	0	2	**11**	5	5	1	19	0.111
UNK	0	0	0	**4**	0	0	0	0	0	0	0	0.418

2.3.4.1.2 Diversity indices

Tall pure mopane woodland, short mixed mopane woodland and closed *Acacia erioloba* savanna were the largest groups with 45, 41 and 68 sites respectively while closed *Acacia-Combretum* woodland and closed mixed *Acacia* veld were the smallest with only 3 and 2 sites respectively. According to Hill's N1 and N2 diversity indices tall mixed broadleaf woodland had the greatest diversity of both abundant and very abundant species. All groups, except for tall mixed mopane woodland and closed mixed *Acacia* veld had similar values for Hill's N1 and N2. Both tall pure mopane woodland and closed mixed *Acacia* veld had a substantially greater diversity of abundant species than very abundant species, although the accuracy of the estimate for closed mixed *Acacia* veld is questionable, owing to the group size. Short mixed broadleaf woodland, open mixed *Acacia*

veld, closed *Acacia-Combretum* woodland, closed mixed *Acacia* veld, closed *Acacia erioloba* savanna, tall mixed broadleaf woodland, open *Acacia erioloba* savanna and palm thornveld had similar values for Pielou's evenness ranging from 0.2 to 0.3 indicating that certain species tend to dominate. Tall mixed mopane woodland and short mixed mopane woodland had a slightly lower Pielou's evenness value, while tall pure mopane woodland had the lowest at 0.08 indicating that the species composition was comprised of a small number of dominant species (Table 2.4). This was supported by the mean and maximum species richness, both of which are low (Table 2.1).

Table 2.4: Number of sites and diversity indices for the vegetation types of NG33 and NG34

	Number of sites	Hill's N1	Hill's N2	Pielou's evenness
Tall pure mopane woodland	45	1.3	1.1	0.1
Tall mixed mopane woodland	18	2.0	0.4	0.2
Short mixed mopane woodland	41	3.0	3.2	0.2
Short mixed broadleaf woodland	24	3.9	3.5	0.3
Open mixed *Acacia* veld	9	3.9	3.5	0.2
Closed *Acacia-Combretum* woodland	3	4.0	3.3	0.3
Closed mixed *Acacia* veld	2	4.9	4.0	0.2
Closed *Acacia erioloba* savanna	68	2.9	2.4	0.2
Tall mixed broadleaf woodland	13	4.9	4.6	0.3
Open *Acacia erioloba* savanna	19	3.2	3.0	0.2
Palm thornveld	21	3.5	3.3	0.3

2.3.5 Tree Physiognomy

The within group similarity for all groups was fairly high with tall pure mopane woodland, tall mixed mopane woodland, short mixed mopane woodland, short mixed broadleaf woodland, closed *Acacia erioloba* savanna and tall mixed broadleaf woodland having a within group similarity of greater than 70% (Table 2.5). Open mixed *Acacia* veld and palm thornveld had a within group similarity of greater than 60% while open *Acacia erioloba* savanna was the most variable group with a within group similarity of 59%. Pielou's evenness values for all groups were greater than 0.8 indicating that no one height class was particularly dominant (Table 2.5).

Table 2.5: Mean abundance of height classes (±SE), within group similarity calculated using analysis of similarities (ANOSIM) and Pielou's evenness in the vegetation types of NG33 and NG34. * indicates groups that were excluded from the analysis due to a limited number of sample plots within the group

	HT1 (<0.5m)	HT2 (0.5 - 0.99m)	HT3 (1 – 1.99m)	HT4 (2-2.99m)	HT5 (>3m)	Within group similarity (%)	Pielou's evenness
Tall pure mopane woodland	9 ± 0.7	13 ± 1.0	20 ± 1.6	23 ± 1.4	34 ± 2.7	72	0.9
Tall mixed mopane woodland	8 ± 1.5	11 ± 1.1	21 ± 2.2	23 ± 2.2	37 ± 3.7	74	0.9
Short mixed mopane woodland	10 ± 1.3	13 ± 1.4	24 ± 1.8	26 ± 1.5	28 ± 2.5	71	0.9
Short mixed broadleaf woodland	5 ± 1.0	9 ± 0.9	27 ± 2.5	34 ± 2.6	25 ± 2.6	74	0.9
Open mixed *Acacia* veld	4 ± 1.3	6 ± 1.1	17 ± 2.9	33 ± 6.5	39 ± 8.6	65	0.8
Closed *Acacia-Combretum* woodland	3 ± 1.7	7 ± 1.7	27 ± 6.7	35 ± 2.9	28 ± 4.4	*	*
Closed mixed *Acacia* veld	10 ± 0.0	13 ± 2.5	28 ± 12.5	33 ± 12.5	15 ± 0.0	*	*
Closed *Acacia erioloba* savanna	3 ± 0.4	6 ± 0.5	17 ± 1.5	24 ± 1.5	49 ± 2.6	71	0.8
Tall mixed broadleaf woodland	5 ± 1.8	7 ± 0.7	19 ± 3.4	25 ± 3.0	45 ± 5.5	71	0.8
Open *Acacia erioloba* savanna	4 ± 1.7	8 ± 1.0	26 ± 2.5	26 ± 4.0	37 ± 6.0	59	0.8
Palm thornveld	3 ± 1.1	9 ± 1.8	28 ± 3.5	36 ± 4.0	23 ± 4.1	64	0.9

The most unique groups in terms of structural composition were tall pure mopane woodland, short mixed broadleaf woodland and closed *Acacia* erioloba savanna. These groups were significantly different to all but three, two and three other groups respectively. Tall mixed broadleaf woodland was the least unique and was significantly different to only short mixed broadleaf woodland (Table 2.6).

At a 5 % level no significant difference was found between tall pure mopane woodland, tall mixed mopane woodland and short mixed mopane woodland (Table 2.6). These three groups occurred close to one another in ordination space (Figure 2.4) and had similar abundances of height classes one to four (Table 2.5). Tall pure mopane woodland and tall mixed mopane woodland had a slightly greater abundance of height class five than short mixed mopane woodland (Table 2.5). The

structural composition of short mixed broadleaf woodland was significantly different to all groups except short mixed mopane woodland and palm thornveld. Short mixed broadleaf woodland and palm thornveld occurred close to one another in ordination space and all three were located to the right of axis two (Figure 2.4). Both short mixed broadleaf woodland and palm thornveld showed a dominance of plants in height class four, while short mixed mopane woodland had similar mean abundances in height classes four and five. All three of these groups showed similar abundances of plants in height class three. The other groups all had the greatest abundance of plants in height class five (Table 2.5).

Table 2.6: Significance of pairwise comparisons of height structure adjusted to control for false discovery rate and percentage dissimilarity between groups. Values in bold are significant. B - Tall pure mopane woodland, C - Tall mixed mopane woodland, D - Short mixed mopane woodland, E - Short mixed broadleaf woodland, F - Open mixed *Acacia* veld, H - Closed mixed *Acacia* veld, I - Closed *Acacia erioloba* savanna, J - Tall mixed broadleaf woodland, K - Open *Acacia erioloba* savanna and L - Palm thornveld. Closed *Acacia-Combretum* woodland and closed mixed *Acacia* veld were excluded from the analysis due to a limited number of sample plots within the group

	p- values								Dissimilarity between groups (%)							
	B	C	D	E	F	I	J	K	B	C	D	E	F	I	J	K
B																
C	0.814								26							
D	0.204	0.914							29	28						
E	**0.001**	**0.020**	0.218						30	28	29					
F	**0.007**	**0.018**	**0.013**	**0.018**					34	32	35	33				
I	**<0.001**	**0.072**	**<0.001**	**<0.001**	0.116				33	30	35	35	32			
J	0.107	0.307	0.220	**0.009**	0.206	0.382			30	27	32	31	32	29		
K	**0.001**	0.188	**0.007**	**0.004**	0.750	**0.006**	0.970		36	34	37	35	37	36	34	
L	**<0.001**	**0.003**	**0.003**	0.158	0.149	**<0.001**	**0.049**	0.068	36	35	35	30	38	40	37	40

The structural composition of palm thornveld was more variable than short mixed broadleaf woodland as it had a lower within group similarity (Table 2.5). As a result of this, palm thornveld was not significantly different from open mixed *Acacia* veld, tall mixed broadleaf woodland and open mixed *Acacia* erioloba savanna, all of which are dominated by plants in height class five with abundances of greater than 37%, despite occurring some distance from these three groups in ordination space (Figure 2.4 and Table 2.5). At a 5% level closed *Acacia erioloba* savanna was not significantly different from tall mixed mopane woodland, open mixed *Acacia* veld and tall mixed broadleaf woodland. However at a 10% level, closed *Acacia erioloba* savanna was different from tall mixed mopane woodland ($p = 0.072$) (Table 2.6), as tall mixed mopane woodland had only 60%

of its mean abundance in height classes four and five, while closed *Acacia erioloba* savanna had more than 70% mean abundance in these two height classes (Table 2.5).

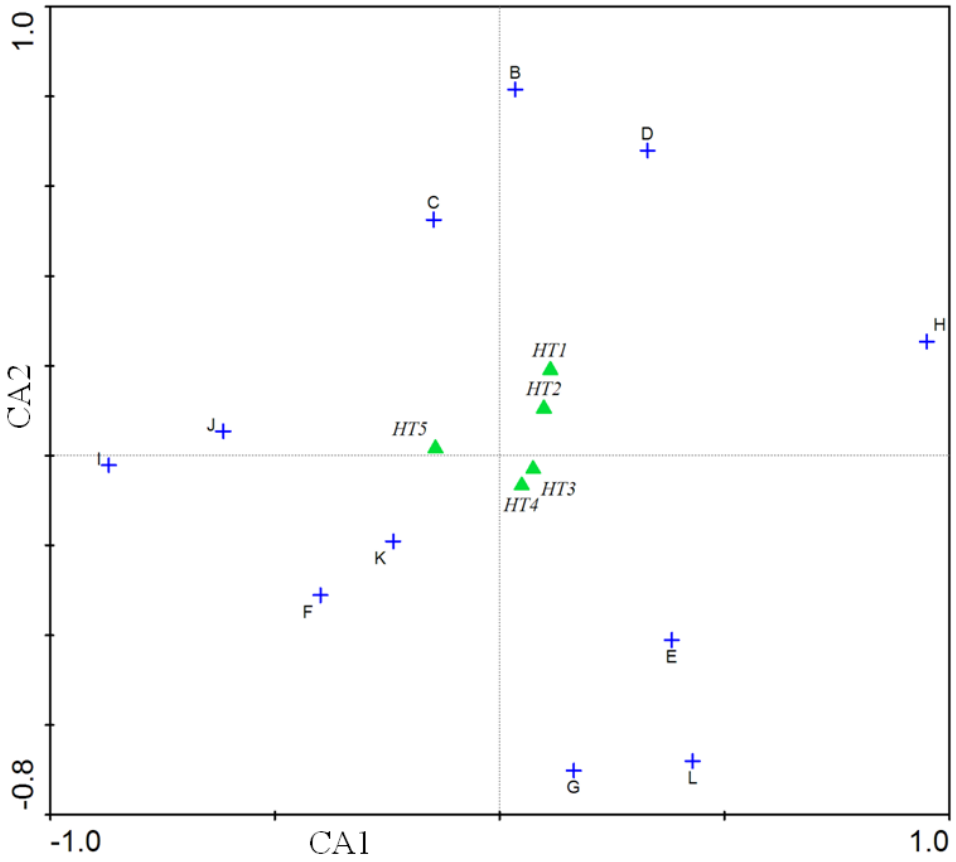

Figure 2.4: Correspondence analysis (CA) of mean height class abundance in the vegetation types of NG33 and NG34. The eigenvalues of axes one and two are 0.042 and 0.019, representing a cumulative variance of 94.9%. Height Classes: HT1 = <0.5m. HT2 = 0.5-0.99m, HT3 = 1-1.99m, HT4 = 2-2.99m and HT5 = >3m. B - Tall pure mopane woodland, C - Tall mixed mopane woodland, D - Short mixed mopane woodland, E - Short mixed broadleaf woodland, F - Open mixed *Acacia* veld, G - Closed *Acacia-Combretum* woodland, H - Closed mixed *Acacia* veld, I - Closed *Acacia erioloba* savanna, J - Tall mixed broadleaf woodland, K - Open *Acacia erioloba* savanna and L - Palm thornveld.

2.3.6 Grass species composition

Urochloa mosambicensis, *Panicum maximum*, *Eragrostis lehmanniana* and *Dactylotenium gigantium* had the widest distribution of the 32 grass species recorded occurring with varying levels

of abundance in all eleven vegetation types (Table 2.7). The grass species composition in the three *C. mopane* dominated vegetation types, tall pure mopane woodland, tall mixed mopane woodland and short mixed mopane woodland, was fairly diverse with between 16 and 28 species present. These three groups had three, four and six dominant species with a cover of greater than 10% respectively. *Urochloa mosambicensis* was the most dominant species in both tall pure mopane woodland and tall mixed mopane woodland. *Eragrostis lehmanniana* also occurred in both groups, with tall pure mopane woodland having a greater cover than tall mixed mopane woodland. Tall pure mopane woodland had some cover of *Aristida congesta*, while tall mixed mopane woodland had substantial cover of *Panicum maximum* and some cover of *Dactylotenium gigantium*. The six dominant species in Short mixed mopane woodland; *D. gigantium*, *E. lehmanniana, P. maximum, P. squarrosa, Stipagrostis hirtigluma* and *U. mosambicensis* contributed similar levels of cover to the sward (Table 2.8).

Closed *Acacia erioloba* savanna also had a diverse cover of grass species with 21 species present. *Dactylotenium gigantium* and *Digitaria eriantha* were the most dominant species with the three other dominant species, *E. lehmanniana, P. maximum* and *U. mosambicensis* occurring at similar densities in the sward (Table 2.8). The grass cover in short mixed broadleaf woodland, open mixed *Acacia* veld, tall mixed broadleaf woodland, open *Acacia erioloba* savanna and palm thornveld comprised between 14 and 17 species. Short mixed broadleaf woodland and open mixed *Acacia* veld both had five dominant species, while tall mixed broadleaf woodland, open *Acacia erioloba* savanna and palm thornveld had four, three and two dominant species respectively. Short mixed broadleaf woodland was dominated by *E. lehmanniana*, with moderate abundances of *D. gigantium, P. maximum, P. squarrosa* and *S. hirtigluma*. Both *E. lehmanniana* and *U. mosambicensis* dominated the sward in open mixed *Acacia* veld with moderate cover of *Chloris virgata, Cynodon dactylon* and *D. eriantha*. *Panicum maximum, U. mosambicensis* and *D. gigantium* dominated the sward in tall mixed broadleaf woodland with some cover of *E. lehmanniana*. The dominant grass species in open *Acacia erioloba* savanna was *D. gigantium* with some cover of *U. mosambicensis* and *C. dactylon*, while palm thornveld was dominated by *C. dactylon* and *Eragrostis rigidior* (Table 2.8).

Closed *Acacia-Combretum* woodland and closed mixed *Acacia* veld both had a low number of grass species present. The grass component in closed *Acacia-Combretum* woodland comprised of eleven species and was dominated by *U. mosambicensis* and had moderate cover of *E. lehmanniana* and *P.*

maximum. Only eight grass species occurred in closed mixed *Acacia* veld. The sward was dominated by equal quantities of *E. lehmanniana* and *U. mosambicensis* and with moderate cover of *A. congesta*, *D. gigantium* and *P. maximum*. This low grass species diversity in closed *Acacia-Combretum* woodland and closed mixed *Acacia* veld may be due to the fact that they comprise of only three and two sites respectively (Table 2.8).

Table 2.7: Frequency of grass species in the vegetation types of NG33 and NG34. Species abbreviations are explained in Appendix B

	Tall pure mopane woodland	Tall mixed mopane woodland	Short mixed mopane woodland	Short mixed broadleaf woodland	Open mixed *Acacia* veld	Closed *Acacia-Combretum* woodland	Closed mixed *Acacia* veld	Closed *Acacia erioloba* savanna	Tall mixed broadleaf woodland	Open *Acacia erioloba* savanna	Palm thornveld
ACO	42	39	15	17	0	0	50	10	15	16	5
AJU	0	0	2	4	0	0	0	0	0	16	0
AME	7	6	22	0	0	0	0	0	0	0	5
ADI	2	0	0	0	0	0	0	0	0	0	0
BIR	2	0	0	0	0	0	0	0	0	0	0
CCI	22	11	2	0	0	0	0	3	7	0	0
CVI	16	17	5	4	56	0	50	21	23	37	33
CEX	0	0	0	0	0	0	0	2	0	0	0
CDA	7	11	5	0	33	33	0	27	15	26	62
DGI	53	72	85	83	67	67	100	79	84	74	38
DER	20	44	41	46	56	100	0	66	46	58	24
DIS	2	0	2	38	0	0	0	0	0	11	0
ECL	9	0	0	0	22	0	0	0	7	0	5
ECU	0	0	0	0	0	0	0	1	0	0	0
EEC	0	0	0	0	0	0	0	0	0	0	5
ELE	80	72	61	71	78	100	100	50	69	58	43
ERI	0	0	0	0	0	0	0	7	0	11	33
ESU	9	6	0	0	0	0	0	0	0	0	0
EVI	2	0	0	0	0	0	0	0	0	0	0
HCO	4	11	0	0	0	0	0	0	0	0	0
HDI	0	0	0	0	0	0	0	1	0	0	0
MRE	2	0	22	17	0	33	50	4	8	16	5
PCO	2	0	0	0	0	0	0	1	0	0	0
PMA	51	88	78	75	33	100	50	66	100	42	43
PPA	0	0	0	8	0	0	0	0	0	0	0
PSQ	42	16	51	46	11	33	0	25	31	11	29
SKA	4	6	15	29	0	33	0	3	15	5	10
SVE	0	0	0	0	11	0	0	0	0	5	0
SBI	2	0	0	0	0	0	0	0	0	0	0
SFE	7	17	0	4	11	0	0	6	8	11	10
SIO	2	0	0	4	11	0	0	1	0	0	0
SHI	18	22	59	54	0	33	50	18	23	21	14
SFI	13	6	0	0	11	33	0	4	8	0	0
TBR	9	0	0	0	0	0	0	0	0	0	0
UMO	78	67	59	38	67	100	100	56	77	79	29
USP	4	6	0	0	11	0	0	0	0	0	0

Table 2.8: Mean abundance of grass species (±SE) in the vegetation types of NG33 and NG34. Species abbreviations are explained in Appendix B

	Tall pure mopane woodland	Tall mixed mopane woodland	Short mixed mopane woodland	Short mixed broadleaf woodland	Open mixed *Acacia* veld	Closed *Acacia-Combretum* woodland	Closed mixed *Acacia* veld	Closed *Acacia erioloba* savanna	Tall mixed broadleaf woodland	Open *Acacia erioloba* savanna	Palm thornveld
ACO	10 ± 2.4	6 ± 2.4	2 ± 0.7	2 ± 1.0	0 ± 0.0	0 ± 0.0	10 ± 10.0	2 ± 0.6	1 ± 0.8	3 ± 1.5	1 ± 0.7
AJU	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.4	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	1 ± 0.6	0 ± 0.0
AME	1 ± 0.7	0 ± 0.3	4 ± 1.5	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	1 ± 1.2
ADI	1 ± 0.7	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0
BIR	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0
CCI	2 ± 0.5	1 ± 1.1	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	1 ± 0.6	0 ± 0.0	0 ± 0.0	0 ± 0.0
CVI	2 ± 0.9	3 ± 1.7	1 ± 0.3	1 ± 0.8	13 ± 4.5	0 ± 0.0	3 ± 2.5	4 ± 1.3	3 ± 1.8	10 ± 3.5	6 ± 2.0
CEX	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.3	0 ± 0.0	0 ± 0.0	0 ± 0.0
CDA	1 ± 0.6	1 ± 0.8	1 ± 0.5	0 ± 0.0	12 ± 6.4	7 ± 6.7	0 ± 0.0	6 ± 1.6	3 ± 2.4	11 ± 4.7	27 ± 5.8
DGI	8 ± 1.4	11 ± 2.3	16 ± 2.2	12 ± 1.8	9 ± 3.4	8 ± 4.4	15 ± 0.0	17 ± 1.8	19 ± 3.6	20 ± 4.5	6 ± 2.0
DER	4 ± 1.5	8 ± 3.0	4 ± 1.0	7 ± 2.2	12 ± 4.3	8 ± 3.3	0 ± 0.0	17 ± 2.6	7 ± 2.2	9 ± 2.4	6 ± 2.7
DIS	0 ± 0.0	0 ± 0.0	0 ± 0.0	5 ± 1.8	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	1 ± 0.7	0 ± 0.0
ECL	1 ± 0.3	0 ± 0.0	0 ± 0.0	0 ± 0.0	1 ± 0.7	0 ± 0.0	0 ± 0.0	0 ± 0.0	1 ± 1.2	0 ± 0.0	0 ± 0.0
ECU	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0
EEC	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0
ELE	19 ± 2.8	13 ± 2.8	17 ± 3.0	18 ± 3.1	17 ± 4.3	15 ± 10.0	25 ± 15.0	13 ± 2.2	13 ± 3.9	8 ± 2.1	10 ± 3.0
ERI	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	1 ± 0.5	0 ± 0.0	2 ± 1.6	15 ± 5.0
ESU	1 ± 0.4	1 ± 1.1	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0
EVI	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0
HCO	0 ± 0.0	1 ± 0.9	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0
HDI	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0
MRE	0 ± 0.0	0 ± 0.0	2 ± 0.6	2 ± 0.9	0 ± 0.0	2 ± 1.7	5 ± 5.0	0 ± 0.0	1 ± 0.8	3 ± 2.0	1 ± 0.7
PCO	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0
PMA	7 ± 1.4	19 ± 2.7	14 ± 1.6	14 ± 3.0	4 ± 2.3	15 ± 2.9	15 ± 15.0	13 ± 1.5	22 ± 4.2	6 ± 2.6	6 ± 2.4
PPA	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.3	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0
PSQ	9 ± 2.1	4 ± 2.9	13 ± 2.7	12 ± 4.4	1 ± 0.6	2 ± 1.7	0 ± 0.0	5 ± 1.5	5 ± 2.3	2 ± 1.7	4 ± 1.9
SKA	0 ± 0.0	0 ± 0.3	4 ± 2.2	4 ± 1.7	0 ± 0.0	7 ± 6.7	0 ± 0.0	0 ± 0.0	2 ± 1.3	1 ± 1.0	5 ± 4.3
SVE	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	1 ± 1.1	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0
SBI	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0
SFE	1 ± 0.3	3 ± 2.0	0 ± 0.0	1 ± 1.3	2 ± 2.2	0 ± 0.0	0 ± 0.0	1 ± 0.7	1 ± 1.2	2 ± 2.1	3 ± 2.9
SIO	0 ± 0.0	0 ± 0.0	0 ± 0.0	1 ± 0.6	1 ± 1.1	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0
SHI	5 ± 2.3	5 ± 2.6	10 ± 2.3	15 ± 4.4	0 ± 0.0	3 ± 3.3	3 ± 2.5	2 ± 0.7	2 ± 0.9	4 ± 2.0	2 ± 1.0
SFI	1 ± 0.5	0 ± 0.0	0 ± 0.0	0 ± 0.0	1 ± 1.1	2 ± 1.7	0 ± 0.0	0 ± 0.0	1 ± 0.8	0 ± 0.0	0 ± 0.0
TBR	1 ± 0.3	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0
UMO	25 ± 3.7	21 ± 5.3	12 ± 2.0	6 ± 1.8	24 ± 7.8	32 ± 9.3	25 ± 5.0	14 ± 2.0	19 ± 3.7	17 ± 3.4	6 ± 2.3
USP	0 ± 0.0	3 ± 2.8	0 ± 0.0	0 ± 0.0	2 ± 2.2	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0

2.3.7 Vegetation type descriptions

Tall pure mopane woodland (Figure 2.5) is dense and almost solely comprised of medium to tall *Colophospermum mopane*. Some *Acacia, Combretum* and *Grewia* species may be found growing in low densities in the understory. The grass layer is dominated by *U. mosambicensis, E. lehmanniana* and *A. congesta*. Tall pure mopane woodland occurs predominantly in NG34 north of the border of NG33 and inside the eastern boundary of NG34 (Figure 2.16).

Tall mixed mopane woodland (Figure 2.6) is less dense than tall pure mopane woodland. It is also dominated by *C. mopane* with some *A. erioloba* being found in open patches. Some other species which may be found occurring in low densities in the understory are *A. hebeclada, A. luederitzii*, *Boscia albitrunca, Combretum* species and *Terminalia sericea*. The grass layer is dominated by *U. mosambicensis* but also includes moderate cover of *E. lehmanniana, P. maximum* and *D. gigantium*. Tall mixed mopane woodland occurs mainly in the central and eastern regions of NG34 along the edges of the tall pure mopane woodland (Figure 2.16).

Short mixed mopane woodland (Figure 2.7) is the least dense of the three mopane dominated vegetation types. *C. mopane* comprises approximately one third of the woody cover with the remainder a mix of *Acacia* species, *Boscia albitrunca*, *Grewia* species, *Lonchocarpus nelsii* and *T. sericea*. The grass sward composition is variable and may be comprised of combinations of *D. giganteum, E. lehmanniana, P. maximum, P. squarrosa, S. hirtigluma* and *U. mosambicensis*. Short mixed mopane woodland occurs in large patches in NG34 south of the boundary of NG33 and east of the Gomoti River and small patches on the boundaries of tall pure mopane woodland and tall mixed mopane woodland in the central and northern sections of NG34 (Figure 2.16).

Tall mixed broadleaf woodland (Figure 2.8) is characterised by a combination of tall *A. erioloba* with an understory of *C. megalobotrys*. Some occurrences of *C. mopane, C. imberbe, Gymnosporia senegalensis, L. nelsii, R. tenuinervis* and *Z. mucronata* may also occur. The grass layer is dominated by *P. maximum, U. mosambicensis* and *D. giganteum* with some patches of *E. lehmanniana*. Tall mixed broadleaf woodland has a scattered distribution in NG34, mainly east of the NG33 boundary and in central and western NG33 along the Moremi Game Reserve boundary (Figure 2.16).

Short mixed broadleaf woodland (Figure 2.9) is characterised by the presence of *L. nelsii, T. sericea* and *D. cinerea*. *Acacia* species, *B. albitrunca* and *C. mopane* may also be found growing at low densities. The grass sward is dominated by *E. lehmanniana* with moderate cover of *D. giganteum, P. maximum, P. squarrosa* and *S. hirtigluma*. Short mixed broadleaf woodland occurs mainly between the southern tip of NG33 and the southern buffalo fence with some patches occurring east of the boundary of NG33 and along the cutline between NG33 and Moremi Game Reserve (Figure 2.16).

Closed Acacia-Combretum woodland (Figure 2.10) is dominated by *A. erioloba* and *C. imberbe* with *A. hebeclada, B. mosambicensis, C. mopane, C. megalobotrys, Gymnosporia senegalensis, H. petersiana* and *Rhus tenuinervis* occurring in low densities. The grass layer is mainly *U. mosambicensis* with small patches of *E. lehmanniana* and *P. maximum*. Closed Acacia-Combretum woodland occurs in small patches in central and western NG34 (Figure 2.16).

Open mixed *Acacia* veld (Figure 2.11) is characterised by the presence of widely scattered individuals of *A. hebeclada* and *A. luederitzii* growing with *A. erioloba.* Other species that may be found in low densities include *Boscia mosambicensis, C. mopane, C. imberbe, Croton megalobotrys, Diospyros lycioides* and *L. nelsii*. The grass cover is combination of *U. mosambicensis* and *E. lehmanniana* with some occurrences of *Chloris virgata, C. dactylon* and *D. eriantha*. Open mixed *Acacia* veld occurs mainly along the northern boundary of NG33 and 34, in small patches in the central and eastern regions of NG34 and east of the Gomoti River in Moremi Game Reserve, north of the NG34 boundary (Figure 2.16).

Closed mixed *Acacia* veld (Figure 2.12) has a higher density of trees than open mixed *Acacia* veld and is characterised by the presence of *A. nigrescens, A. hebeclada* and *B. albitrunca* growing with *A. erioloba*. The grass layer is a combination of *E. lehmanniana* and *U. mosambicensis* with occurrences of *A. congesta, D, gigantium* and *P. maximum*. Closed mixed *Acacia* veld occurs in small patches in south-western NG34 close to the Gomoti River (Figure 2.16).

Closed *Acacia erioloba* savanna (Figure 2.13) is dominated by large *A. erioloba* trees with low densities of *A. hebeclada, C. mopane, C. imberbe, C. megalobotrys, L. nelsii* and *Ziziphus mucronata* in the understory. The grass layer is predominantly *D. gigantium* and *D. eriantha* with some patches of *E. lehmanniana, P. maximum* and *U. mosambicensis*. Closed *Acacia erioloba*

savanna occurs in large patches in central NG33, in NG34 south and east of the NG33 boundary and in smaller patches between the *C. mopane* dominated belts in eastern NG34 (Figure 2.16).

Open *Acacia erioloba* savanna (Figure 2.14) is characterised by a scattered distribution of *A. erioloba* with occasional occurrences of *C. mopane, L. nelsii, T. sericea, A. hebeclada, B. albitrunca, C. imberbe, H. petersiana* and *Z. mucronata*. The grass layer is dominated by *D. giganteum* with some patches of *U. mosambicensis* and *C. dactylon*. Open *Acacia erioloba* savanna occurs in two main patches, firstly in NG34 south of the boundary of NG33 and Moremi Game Reserve and secondly, in central NG34 between the *C. mopane* dominated belt to the north and the closed *Acacia erioloba* savanna to the south (Figure 2.16).

Palm thornveld (Figure 2.15) is characterised by a sparse cover of *Z. mucronata* and *H. petersiana* with some occurrences of *A. erioloba, A. hebeclada, A. nigrescens, C. megalobotrys, D. lycioides, L. nelsii* and *C. imberbe*. The grass cover is a combination of *C. dactylon* and *E. rigidior*. Palm thornveld occurs in the old floodplain regions south of NG33 and east of the Gomoti River (Figure 2.16).

Figure 2.5: Examples of tall pure mopane woodland.

Figure 2.6: Examples of tall mixed mopane woodland.

Figure 2.7: Examples of short mixed mopane woodland.

Figure 2.8: Examples of tall mixed broadleaf woodland.

Figure 2.9: Examples of short mixed broadleaf woodland.

Figure 2.10: Examples of closed *Acacia- Combretum* woodland.

Figure 2.11: Examples of open mixed *Acacia* veld.

Figure 2.12: Examples of closed mixed *Acacia* veld.

Figure 2.13: Examples of closed *Acacia erioloba* savanna.

Figure 2.14: Examples of open *Acacia erioloba* savanna.

Figure 2.15: Examples of palm thornveld.

2.3.8 Mapping

The northern and eastern sections of NG34 are dominated by *C. mopane* (Figure 2.16). Short mixed mopane woodland is the most dominant of the three *C. mopane* vegetation types with an area of 288.73 km^2, followed by tall pure mopane woodland (209.16 km^2) and tall mixed mopane woodland (173.30 km^2) (Table 2.9). These belts of mopane woodland are interspersed with *Acacia* dominated vegetation types (Figure 2.16) with open and closed *A. erioloba* savanna being the most widespread and covering 122.93 km^2 and 73.71 km^2 respectively (Table 2.9). Palm thornveld is limited to the old floodplains along the courses of dry river beds from the Gomoti River east into NG33 (Table 2.9). Tall and short mixed broadleaf woodland comprise a small proportion of the vegetation, 30.67 km^2 and 43.39 km^2 respectively, and occur in small patches in NG33 and central and western NG34 (Figure 2.16).

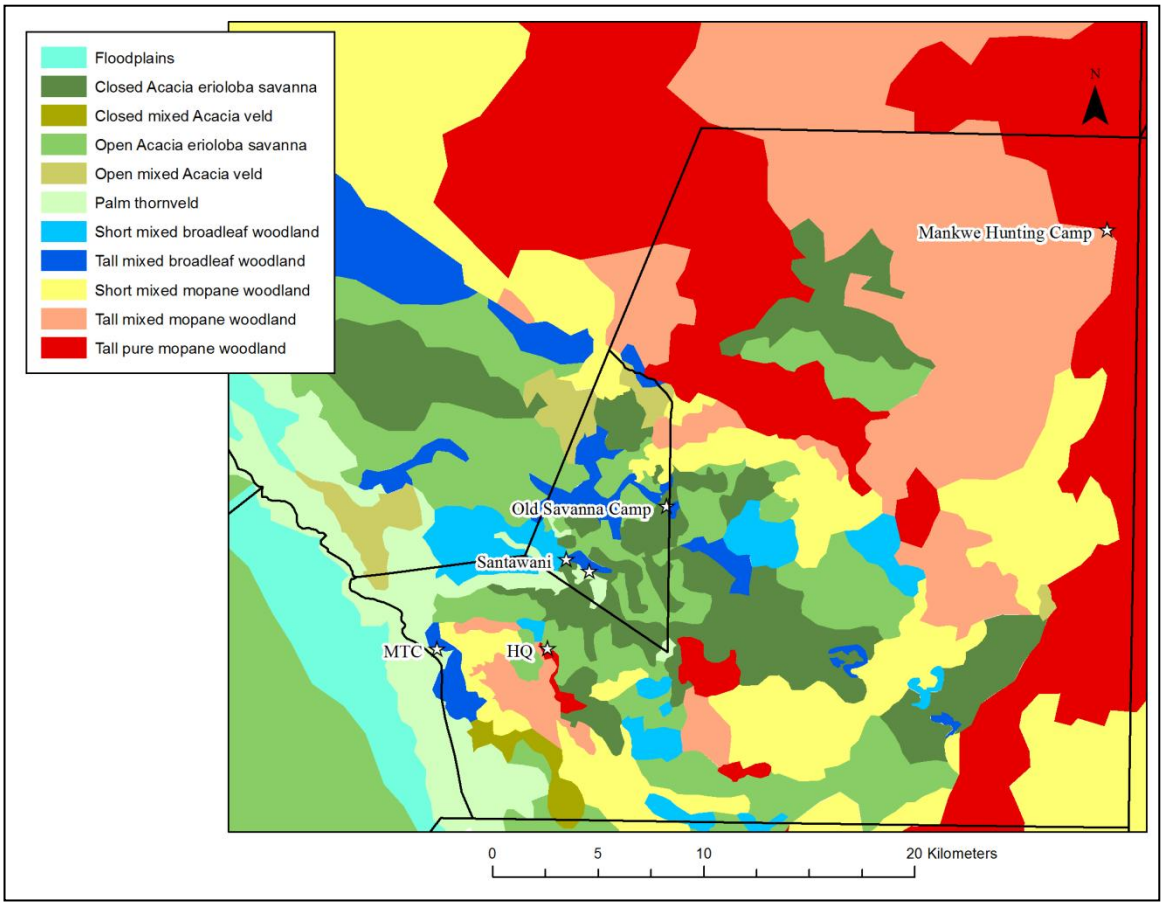

Figure 2.16: Distribution of vegetation types in NG33 and 34. Closed *Acacia-Combretum* woodland is not shown as the distribution is too limited to be visible at this scale.

Table 2.9: Area of the vegetation types in NG33 and NG34

Vegetation Type	Area (km^2)
Open Acacia erioloba savanna	122.93
Closed *Acacia erioloba* savanna	73.71
Open mixed *Acacia* veld	14.01
Closed mixed *Acacia* veld	7.64
Tall mixed broadleaf woodland	30.67
Short mixed broadleaf woodland	43.39
Tall pure mopane woodland	209.16
Tall mixed mopane woodland	173.30
Short mixed mopane woodland	288.73
Palm thornveld	60.41

2.4 DISCUSSION

Overall the vegetation in NG33 and NG34 was short according the broad-scale classification guidelines stated by Edwards (1983). The two most widespread woody species in NG33 and NG34, occurring in varying densities in every vegetation type, were *A. erioloba* and *C. mopane*, while the most widespread grass species were *U. mossambicensis*, *P. maximum*, *D. gigantium* and *E. lehmanniana*.

Short mixed mopane woodland was the most dominant vegetation type in NG33 and NG34 covering an area of 288.73 km^2. It was also one of the least taxonomically variable of the eleven vegetation types, with only tall pure mopane woodland and tall mixed mopane woodland showing less variation. These two vegetation types were also fairly dominant, covering 209.14 km^2 and 173.30 km^2 respectively. Together these three *C. mopane* dominated vegetation types accounted for approximately half the vegetative cover in NG33 and NG34. The majority of the cover in the two tall mopane vegetation types was over 2 m tall with an aerial cover of over 75%, while the cover in short mixed mopane woodland was sparser, with the bulk of the woody vegetation being less than 3 m tall. Despite having the greatest woody cover, tall pure mopane woodland had the lowest mean species richness. Tall mopane tends to occur on nutrient rich alluvial soils (Roodt 1998) and, although slow-growing initially, can reach heights of up to 30m (Venter and Venter 2002). The

structural differences observed between the tall and short *C. mopane* vegetation may be caused by several factors. Nutrient poor, sandy soils (Roodt 1998) and the associated decrease in available moisture can result in stunted *C. mopane* trees (February et al. 2007), while disturbance factors such as fire, wood harvesting and extensive utilization by elephants result in multi-stemmed coppice growth (Van Voorthuizen 1976, Lombard 2003) and may cause the development of short mixed mopane woodland in areas where soil conditions allow for tall mopane woodland.

The nutrient rich, shady environment under tall mopane woodland resulted in the dominance of *U. mossambicensis* observed in the grass sward (Chippindall and Crook 1976, van Oudtshoorn 1999). Surprisingly *P. maximum*, another shade tolerant species favouring alluvial soils (Chippindall and Crook 1976), was largely absent in this dense *C. mopane* dominated vegetation and appeared to increase in cover with decreasing *C. mopane* density. This may be due to the fact that *P. maximum* is a sub-climax to climax perennial species (van Oudtshoorn 1999) relying largely on vegetative reproduction requiring a consistent supply of belowground resources. As *Colophospermum mopane* is an extremely strong belowground competitor (Smit and Rethman 1998, Rathogwa et al. 1999) with more than half of its fine root biomass in the first half a metre of soil (Smit and Rethman 1998), this intense belowground competition may sufficiently affect the available resources to preclude the occurrence of *P. maximum.* By contrast *U. mossambicensis* functions as a pioneer to sub-climax, annual or weak perennial species (Chippindall and Crook 1976, van Oudtshoorn 1999) producing large quantities of viable seed (Erikson and Erikson 1997), affording the species numerous colonisation opportunities. As much of the sward in the *C. mopane* vegetation types appears to be annual (personal observation, 2008) it is possible that *U. mossambicensis* colonises the area in early spring before *C. mopane* begins active growth to replace the leaves lost during winter (Roodt 1998).

The most taxonomically variable vegetation types were palm thornveld, short mixed broadleaf woodland and open mixed *Acacia* veld. Short mixed broadleaf woodland and open mixed *Acacia* veld were similar in that they were both dominated by *A. erioloba*, but were separated by the presence of *T. sericea* and *L. nelsii* in short mixed broadleaf woodland and *A. hebeclada* and *A. luederitzii* in open mixed *Acacia* veld. Palm thornveld was the most variable of the three and most different taxonomically from the other vegetation types. It had sparse woody cover dominated by *Z. mucronata* and *H. petersiana* and the majority of the grass layer comprised the creeping, perennial pioneer *C. dactylon* (Chippindall and Crook 1976, van Oudtshoorn 1999). The 60.41 km^2 of this

vegetation type occurred on the old floodplains east of the Gomoti River with *H. petersiana* and *C. dactylon* being characteristic dry floodplain species, able to tolerate fairly saline soils (Roodt 1998, Heinl et al. 2004).

Closed mixed *Acacia* veld and *Acacia-Combretum* woodland had the most limited distribution with closed mixed *Acacia* veld covering only 7.64 km^2, less than 1% of the total area of NG33 and NG34 and *Acacia-Combretum* woodland patches being too small and scattered to map. One of the reasons *Acacia-Combretum* woodland has such a limited distribution may be that *Combretum* species are heavily utilized by elephants (Ben-Shahar 1993) although, unlike *Acacia* species, *Combretum* species may continue growing after being broken (du Toit et al. 2003). This heavy utilization may explain why *Combretum* species appeared to be limited to dense vegetation, affording them some protection from elephant damage. Both of these vegetation types had a high diversity of very abundant species. In addition closed mixed *Acacia* veld had the highest mean species richness of all eleven vegetation types, despite its limited distribution. The most taxonomically diverse vegetation type overall, was tall mixed broadleaf woodland, with the greatest diversity of both abundant and very abundant species, while the most structurally diverse was open *Acacia erioloba* savanna. This structural diversity may be attributed to the sparse woody cover in open *Acacia erioloba* savanna, allowing for species recruitment.

Of the two previous studies providing taxonomic vegetation type descriptions, the one which is most closely correlated to the eleven vegetation types described here is the oldest classification conducted by Tinley (1966). Seven of the eight vegetation types described by Tinley (1966) can be matched to groups produced by this classification, while the same can be said for only five of the seven groups described by Ringrose et al (2003). The absence of any broadleaf dominated communities in the ecoregions described by Ringrose et al. (2003) and the limited description given by Tinley (1966) emphasises the level of taxonomic variation observed in the dry woodland and savanna vegetation in different regions of the Okavango Delta and emphasises the importance of using detailed field-based vegetation studies in conjunction with remote sensing techniques.

This study not only provides valuable geo-referenced field data to augment the Delta-wide maps produced in 2002 (Ramberg et al. 2006), but also important background data for both the habitat based monitoring projects to be conducted in NG33 and 34 and the carnivore and herbivore research being conducted in the area.

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CHAPTER 3: DEVELOPING A DRY WOODLAND AND SAVANNA FUNCTIONAL TYPE CLASSIFICATION TO FACILITATE VEGETATION MONITORING AND ADAPTIVE MANAGEMENT

3.1 INTRODUCTION

Since the late 1970s there has been increasing emphasis on adaptive management (Holling 1978, Walters 1986). The concept focuses on 'learning by doing' and follows a four step circular system. Firstly a management plan is developed, it is then implemented and the effects monitored, finally the effects of that management strategy are investigated and the management plan is updated with any changes necessary. The updated management plan is then implemented and the process begins again (Allan 2007). In order to effectively conduct any form of adaptive management, an effective monitoring system is essential (Ludwig et al. 2000, Havstad and Herrick 2003). Since the adaptive management concept was first developed, many of these monitoring programs have been established and a large proportion have since been abandoned (Watson and Novelly 2004). This may be due to a lack of funding, personnel or poor design when the program was developed. An effective monitoring program should run for as long as possible and adapt with a changing knowledge base, thus requiring a substantial commitment from the monitoring institution. Possibly the most critical factor in the development of a long-term monitoring program is securing long-term funding. Once this has been secured there needs to be a commitment of both staff and resources to ensure that sampling is conducted and data is correctly recorded, stored and managed in a well structured meta-database. This ensures not only effective monitoring, but also the persistence of the program despite the inevitable staff turnover (Watson and Novelly 2004). The method and frequency of sampling depends on the aims of the program, however methods should be easily repeatable, allowing for minimal user bias and the sampling window should be large enough to accommodate potential delays in fieldwork (Brakenheilm and Qinghong 1995, Watson and Novelly 2004).

A well established, efficiently run monitoring program can then be used to monitor changes resulting from physical ecosystem drivers such as; rainfall, CO_2 levels, available soil nitrogen, flooding, fire, grazing and hunting, social ecosystem drivers such as; changes in land use and occupation, perceptions toward property rights and attitudes towards land management, and economic and policy ecosystem drivers such as; tax laws, environmental policy, trade agreements and government ecosystem management, in terms of both management and compliance to legislation (Brown and Havstad 2003). In addition to detecting changes in the system, a monitoring program can provide data to describe the present environmental conditions, document abnormal events and investigate problems and threats to the

system either seasonally or annually (McDougald et al. 2003). Regardless of the purposes of the monitoring system a detailed set of baseline data is critical to allow for any changes to be detected (McDougald et al. 2003). While taxonomic and structural classifications provide a detailed description of the vegetative composition, such detail is not always necessary at a monitoring and management level. For this reason species or taxonomic classes are grouped into functional types or response groups, which are groups of species that respond to environmental factors and disturbance in a similar way, and increase understanding of how the vegetation as a whole interacts with the environment (Symstad 2002).

In 1997 the Okavango Delta was declared a Ramsar wetland of international importance (Ramsar-Convention-Secretariat 2011). As a result of this in 2002 the Okavango Delta Management Plan (ODMP) project was initiated to ensure the conservation and sustainable use of the Okavango Delta (Jansen and Madzwamuse 2003). The ODMP identified 12 resource components and the institutions responsible for them as critical to the sustainable management of the Okavango Delta. One of the primary components identified was the vegetation resources, which fall under the Ministry of Environment, Wildlife and Tourism's Department of Forestry and Range Resources. The department is expected 'to ensure sustainable management of the Okavango Delta vegetation initiated and supported by providing accurate data and assisting in resolving vegetation management conflicts' (Trollope et al. 2006).

The ODMP states that the development of a monitoring program is essential to provide a scientific grounding for adaptive management, in order to mitigate the perceived threats to the ecosystem resulting from tourism and other local activities (Jones et al. 2009). Ringrose et al. (2003) list seven areas of study, highlighted in numerous publications over the last two decades, in which some form of monitoring would benefit the scientific communities understanding of the functioning of the Okavango Delta system. These include monitoring changes in the floodwater inflow and the principal direction of flooding, changes in floodplain vegetation composition and soil properties, effects of fire, effects of grazing and browsing on the floodplain and riparian forest vegetation and the effect of elephant utilization, type of land utilization and veterinary cordon fences on the dryland vegetation (Ringrose et al. 2003). These dryland savannas surrounding the Okavango Delta provide many essential ecosystem services such as, tourism opportunities, grazing and veld products to Botswana's growing population and are vulnerable to overexploitation. In addition the woodland savannas of southern Africa are classified as one of the top ten global tipping point regions with regard to changes in biodiversity and the resulting effects on climate and the biodiversity of other regions (Finckh and Schmiedel 2010).

In order to conduct these monitoring programmes and effectively manage the vegetation, a simple and practical vegetation map, supported by a comprehensive assessment of the woody and herbaceous vegetation (Trollope et al. 2006), as well as a description of the underlying soils is essential. This map should contain a broad classification above the standard vegetation classification with vegetation management units based on plant morphology and the dominant vegetation types (Good et al. 1993).

There are currently two broad-scale vegetation classifications of the Okavango Delta. One of the more commonly used broad classification systems is described by Mendelsohn and el Obeid (2004) (Trollope et al. 2006). Their classification covers the entire Delta system from the catchment in the Angolan highlands to the Delta floodplains. The region covered is so extensive and the vegetation classes so broad that the vegetation of the Delta comprises only five vegetation units with the dry woodland and savanna in the southern Delta divided into only two units, *Mopane* woodland dominating the north-eastern regions and *Acacia* woodland dominating the south-eastern regions (Mendelsohn and el Obeid 2004). This classification is too broad and encompasses too much variation within the vegetation units to be useful for research and monitoring purposes required to fulfil the requirements of the Okavango Delta Management Plan (Jansen and Madzwamuse 2003). By contrast the original Okavango Delta taxonomic vegetation classification of 45 vegetation types (Trollope et al. 2006) is too detailed for use as functional types or management units map. Establishing monitoring programs in each of these vegetation types would be too costly and time consuming to be effective. For this reason Jellema et al. (2002) developed a Delta-wide classification comprising ten vegetation types. While this number of groups is more manageable, the classification covers all vegetation types occurring within the delta resulting in an increased level of simplification within the vegetation types described. In addition the level of variation within the groups is inconsistent, making them difficult to use for management and monitoring purposes.

The objectives of this chapter were (1) to create a classification of dry woodland and savanna vegetation functional types, (2) to map the geographical distribution of these functional types or vegetation management units (VMU) in NG33, NG34 and Moremi Game Reserve, (3) to determine the relationship between the topsoil and subsoil characteristics underlying these vegetation management units, (4) to describe the soil characteristics underlying these vegetation management units and to determine the effect of those soil characteristics on the occurrence of dominant woody and herbaceous species.

3.2 METHODS

3.2.1 Classification of functional types

The data used to develop the vegetation classification in chapter two were re-examined and each species, except *Colophospermum mopane*, was categorised according to leaf morphology as either micropyllous or broadleaf. Owing to the abundance of *C. mopane* this species was allocated a separate leaf morphology category. These data was then subjected to an agglomerative, hierarchical cluster analysis (ACL) (in the software program PRIMER (Clarke and Gorley 2006)) using the group mean and Bray-Curtis similarity to create groups. Groups were defined according to a 65% similarity level. The sites were then categorised according to the twelve vegetation types described in chapter two. The group which had the greatest frequency of sites from a particular vegetation type was then allocated that vegetation type.

3.2.2 Mapping

The geographical distribution of these groups or vegetation management units (VMU) was then mapped in ArcMap 10 (ESRI 2010) using aerial photographs obtained from the Okavango Research Institute (ORI) and the previously mapped geographical distribution of the vegetation types.

3.2.3 Data Collection

Owing to time constraints for data collection and the need for rapid data collection for the purposes of long term monitoring, sixteen sites for the establishment of long-term monitoring points were identified within each of the VMUs (Figure 3.3). These sites were located within NG33, NG34 and Moremi Game Reserve, three areas adjacent to one another and thus receiving similar rainfall and with similar underlying soil types. These areas are all exclusively utilized by wildlife and there are no fences separating these areas so there a few differences in terms of animal number, animal types and animal movement.

3.2.3.1 Vegetation

The methods used to sample the vegetation at each of these sites were a modified version of those used by Dahlberg (2000). At each of these sites three transects (100m by 3m) were set out approximately 5m apart in order to prevent overlap. GPS co-ordinates were recorded at the start and end points of each transect to allow for repeat sampling. The species and height class, <0.5m, 0.5-0.99m, 1-1.99m, 2-2.99m and >3m, of each woody plant rooted within the transect area was then recorded. The herbaceous layer was sampled using 1m x 1m quadrats evenly spaced along the transect line. In each quadrat the percentage cover was recorded for each grass species. In addition the total percentage cover was recorded for other herbaceous

species and bare ground. These herbaceous species were defined according to Roodt (1998a) as 'non-woody, seed bearing plants which die down to the ground after flowering'.

3.2.3.2 Soil

At each site, three randomly located topsoil (the top 15cm) and subsoil (below 40 cm) subsamples were taken and combined forming one topsoil and one subsoil sample for each site. Owing to the sandy nature of the soils in the study area these samples were then analysed for particle size composition, sand fraction composition and pH. Soil particles were classed into the following categories, clay (<0.002mm), silt (0.05 – 0.002mm) and sand (2.0 – 0.05mm). In addition infiltration rate was measured using a mini disc infiltrometer manufactured by Decagon Devices, USA. This was done at three randomly selected locations within the sample site to determine a mean infiltration rate for each site.

3.2.4 Data Analysis

3.2.4.1 Topsoil-subsoil relationships

The relationship between topsoil and subsoil characteristics was determined using a Mantel test in PC-ORD (McCune and Mefford 1997) and the correlations between the various soil characteristics were determined using a correlation analysis in GenStat 12 (VSN-International 2009).

3.2.4.2 Soil-VMU relationships

The relationships between the management units and soil characteristics were determined using a permutational multivariate analysis of variance (PERMANOVA) with pairwise comparisons in PRIMER (Clarke and Gorley 2006) and displayed using a principle components analysis (PCA) in CANOCO (ter Braak and Smilauer 1997). The dispersion of sites within each management unit was determined using PERMDISP in PRIMER (Clarke and Gorley 2006).

3.2.4.3 Soil-Species relationships

The relationships between soil characteristics, woody species and sward composition was determined using canonical correspondence analysis (CCA) in CANOCO with manual forward selection using 10 000 permutations in a Monte-Carlo test (ter Braak and Smilauer 1997).

3.3 RESULTS

3.2.1 Classification of functional types

The agglomerative cluster analysis revealed four distinct functional type groups or vegetation management units (VMU), which separate at a similarity level of 65% (Figure 3.1). Both tall pure

mopane woodland and tall mixed mopane woodland were included in unit A, with 98% and 67% of sites classified in this VMU respectively (Table 3.1). Short mixed mopane woodland was the only vegetation type to be classified as unit B with 66% of the sites falling into this VMU (Table 3.1). Open mixed *Acacia* veld (89% of sites), closed mixed *Acacia* veld (100% of sites), closed *Acacia erioloba* savanna (79% of sites) and open *Acacia erioloba* savanna (58% of sites) all fall under unit C, while short mixed broadleaf woodland (63% of sites), closed *Acacia-Combretum* veld (100% of sites), tall mixed broadleaf woodland (100% of sites) and palm thornveld (100% of sites) were all classified as unit D (Table 3.1). The units were then renamed as follows: tall mopane woodland (unit A), shrub mopane woodland (unit B), mixed thornveld (unit C) and mixed broadleaf woodland (unit D).

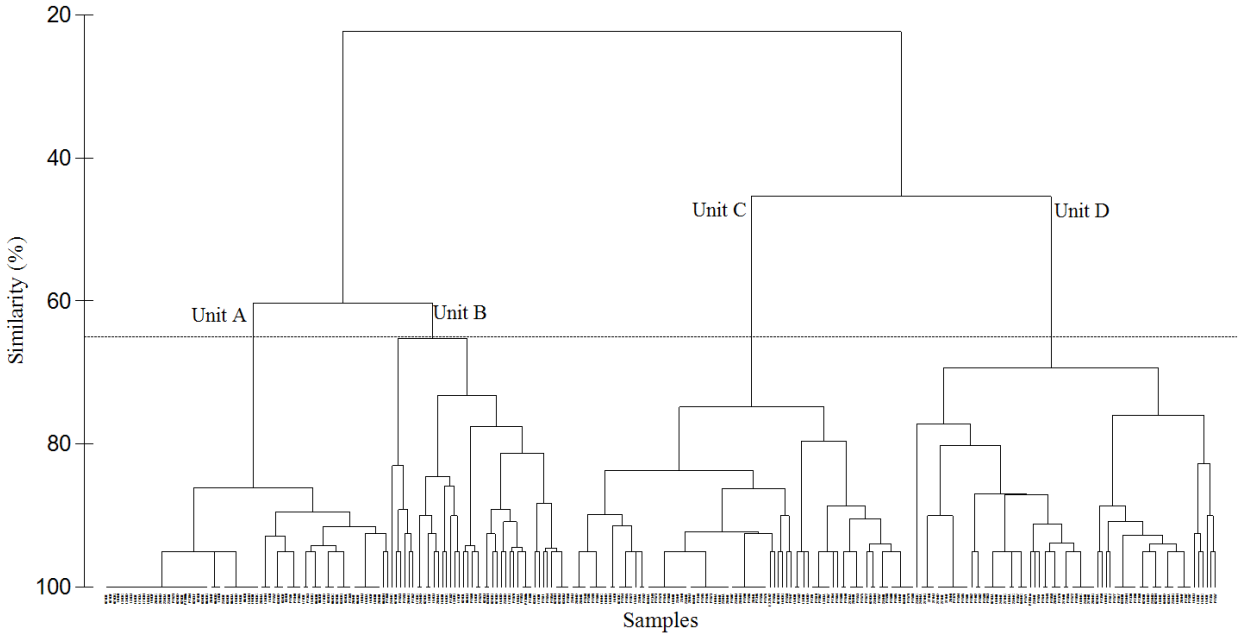


Figure 3.1: Cluster analysis using absolute cover of leaf morphology categories.

Table 3.1: Frequency of sites from each vegetation type occurring in the four vegetation management units, with shading indicating maximum frequency

	Unit A	Unit B	Unit C	Unit D
Tall pure mopane woodland	44	1	0	0
Tall mixed mopane woodland	12	6	0	0
Short mixed mopane woodland	12	27	1	1
Short mixed broadleaf woodland	0	4	5	15
Open mixed *Acacia* veld	0	0	8	1
Closed *Acacia-Combretum* veld	0	0	0	3
Closed mixed *Acacia* veld	0	0	2	0
Closed *Acacia erioloba* savanna	0	3	54	11
Tall mixed broadleaf woodland	0	0	0	13
Open *Acacia erioloba* savanna	0	1	11	7
Palm thornveld	0	0	0	21

3.2.2 Mapping

The vegetation pattern in Moremi Game Reserve is less variable than that observed in NG33 and NG34. A belt of mixed thornveld runs from the north-western corner of Moremi Game Reserve towards the boundary of NG33, parallel to the Gomoti River. This belt becomes interspersed with patches of mixed broadleaf woodland in NG33 and then further fragmented towards central and southern NG34, where patches of shrub mopane woodland and tall mopane woodland appear. A strip of tall mopane woodland runs from west to east, parallel to the Khwai River in northern Moremi. The regions between this and the mixed thornveld belt are comprised of shrub mopane woodland (Figure 3.2).

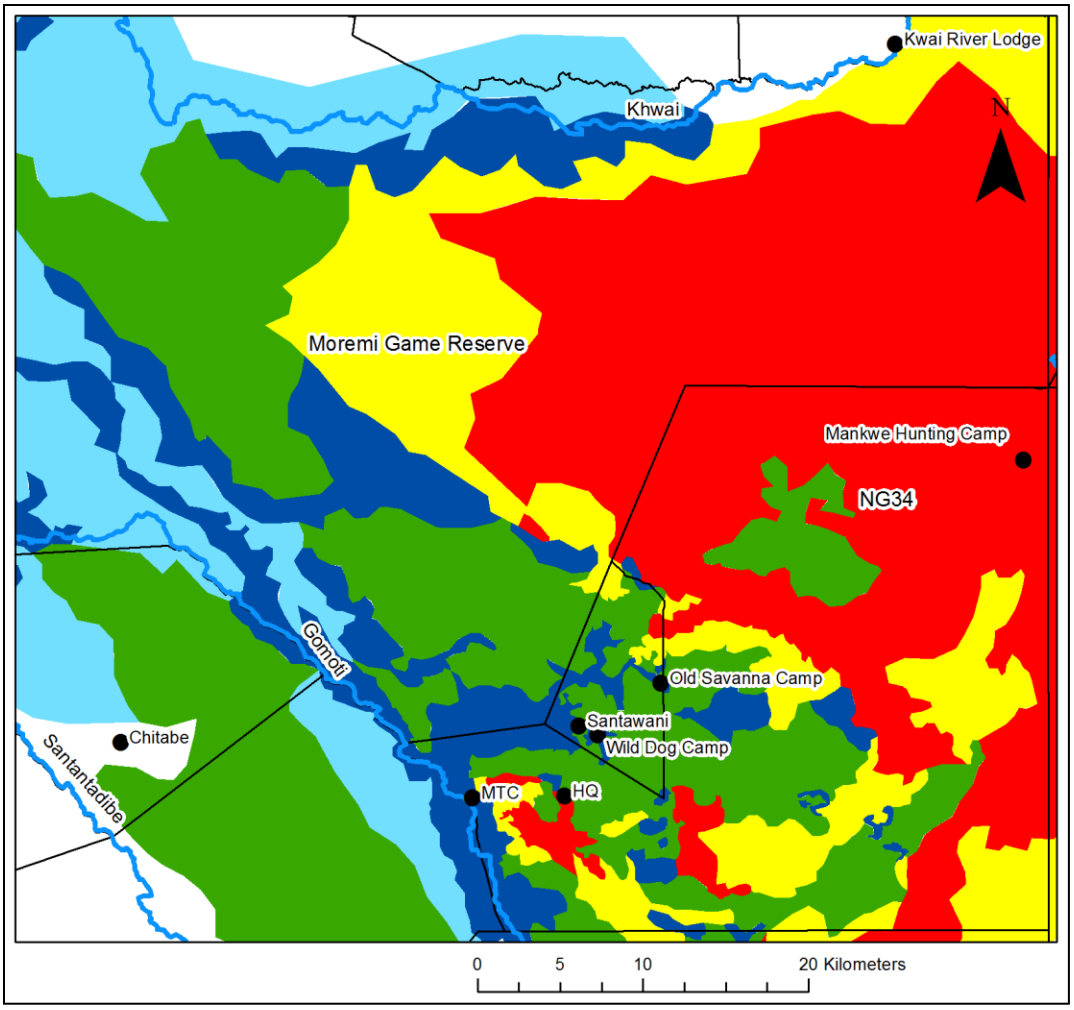


Figure 3.2: Distribution of the vegetation management units, tall mopane woodland (red), shrub mopane woodland (yellow), mixed broadleaf woodland (dark blue) and mixed thornveld (green) in NG33, NG34 and Moremi Game Reserve with floodplain (light blue) regions also shown.

3.2.3 Sampling Points

Within each VMU sixteen monitoring points were established. These points were located in NG33, NG34 and Moremi Game Reserve (Figure 3.3).

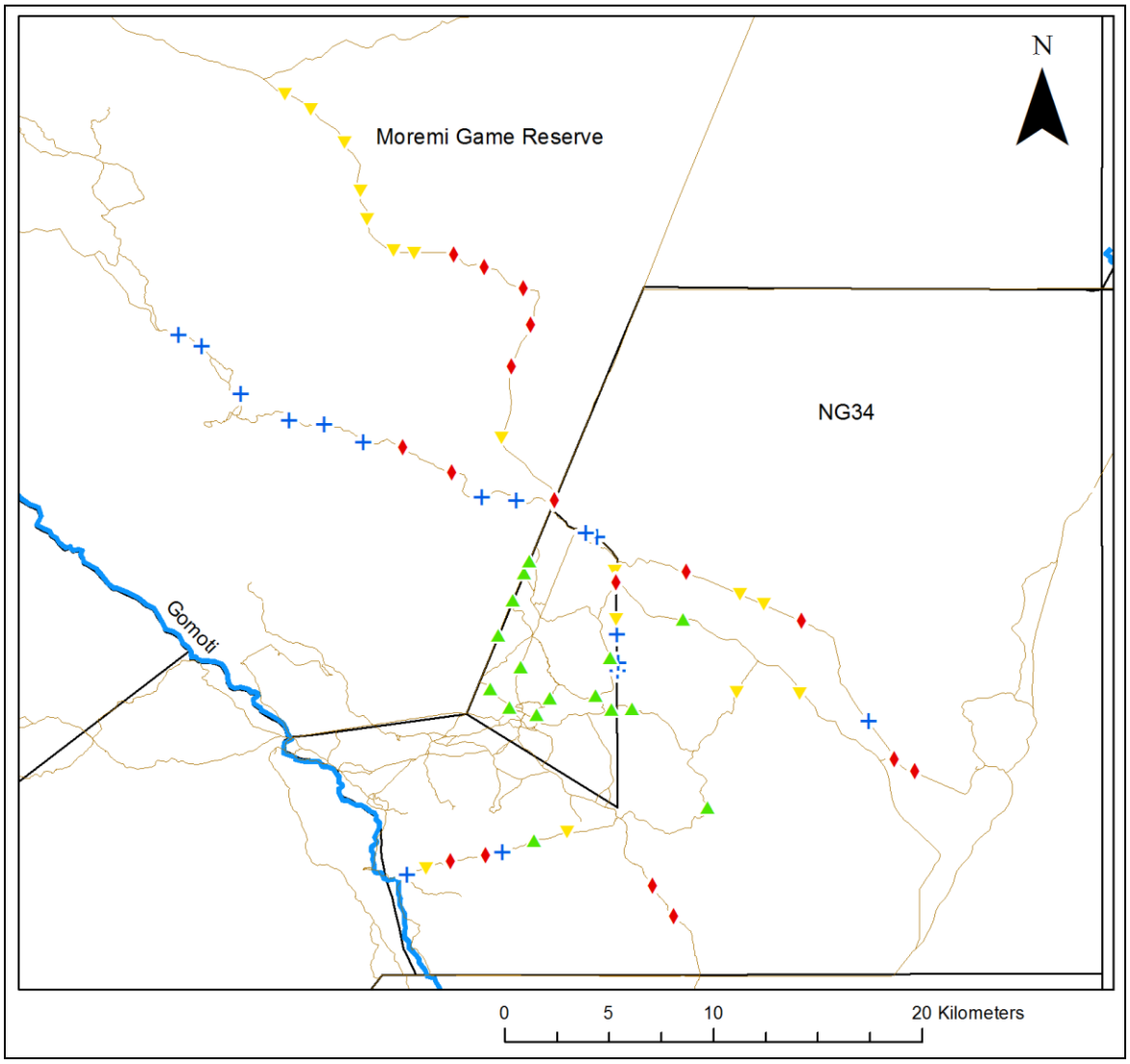


Figure 3.3: Locations of sampling points for tall mopane woodland (♦), shrub mopane woodland (▼), mixed broadleaf woodland (+) and mixed thornveld (▲) in NG33, NG34 and Moremi Game Reserve. Rivers are indicated in blue and roads in brown.

3.2.4 Topsoil-Subsoil relationships

Preliminary examinations of the data, using principle coordinates analysis (PCA), found one of the sites to be an extreme outlier as a result of vastly different topsoil and subsoil sand content measurements. This site was removed from any further analyses. A Mantel test found the topsoil and subsoil qualities to be

closely correlated (r = 0.734057, p = 0.001) and as a result analyses were performed on the topsoil data only. Correlation analysis showed a high positive correlation between topsoil silt and clay content and between topsoil sand content and infiltration (Table 3.2). For this reason silt and clay content, and sand content and infiltration were combined to form two negatively correlated factors which were then used in all further analyses. pH showed a weaker positive correlation to silt and clay and negative correlation to sand and infiltration (Table 3.2). All of these correlations were highly significant. The ordination diagram showed the soil structural composition gradient to be strongly correlated to PCA axis 1 and the pH gradient to be weakly correlated to PCA axis 2 (Figure 3.4).

Table 3.2: Correlations between the soil properties of the topsoil layer across the four vegetation management units, tall mopane woodland, shrub mopane woodland, mixed broadleaf woodland and mixed thornveld

Clay					
Infiltration	-0.616				
Sand	-0.916	0.717			
Silt	0.681	-0.698	-0.918		
pH	0.444	-0.385	-0.460	0.392	
	Clay	Infiltration	Sand	Silt	pH

3.2.5 Soil-VMU relationships

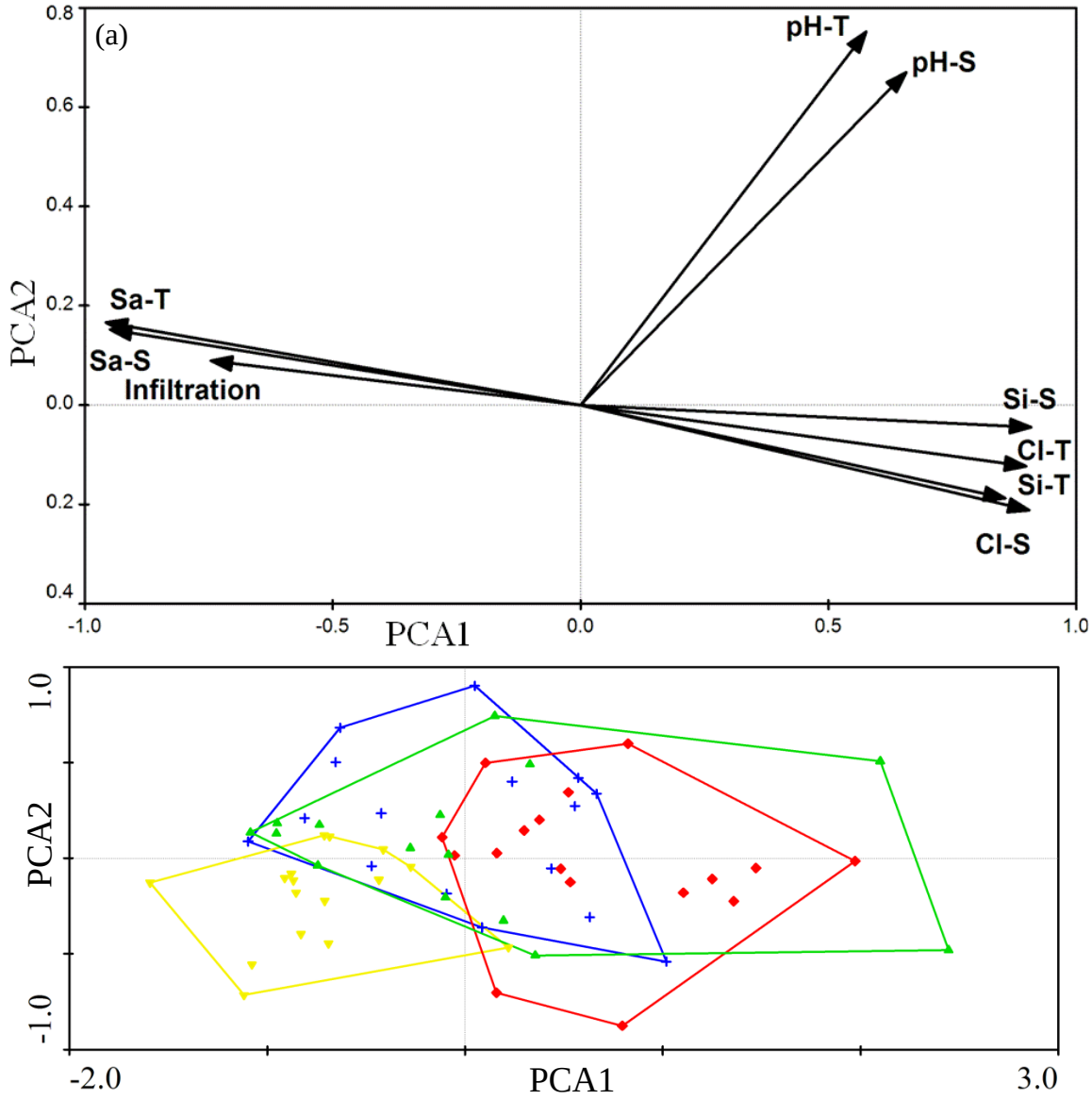
A permutational multivariate analysis of variance (PERMANOVA) found significant differences between the soil properties of the different management units (p(perm) = 0.0001). The dispersion of points in tall mopane woodland and mixed thornveld was not different, while it was in mixed broadleaf woodland and shrub mopane woodland. These two management units represented opposite extremes in point dispersion, with mixed broadleaf woodland having the widest overall spread of points and shrub mopane woodland having the narrowest. The boundaries of mixed thornveld covered a larger area than mixed broadleaf woodland however this was due to two isolated points situated on the far right of the ordination diagram. The majority of the points were clustered close together with the main spread along PCA axis 1 (Figure 3.4).

A PERMANOVA with pairwise comparisons, revealed that the soil properties of tall mopane woodland and shrub mopane woodland were not only significantly different from one another but also to those observed in mixed broadleaf woodland and mixed thornveld. No significant difference was found between the soil properties of mixed broadleaf woodland and mixed thornveld (Table 3.3). These two groups overlapped substantially on the ordination diagram, with the exception of the two isolated sites

sampled in mixed thornveld which ordinate on the far right of PCA axis 2. The mixed broadleaf woodland sites and the majority of the mixed thornveld sites occurred near the centre of the ordination diagram (Figure 3.4) indicating that they had equivalent levels of sand and clay or silt and had an average pH compared to the other vegetation management units (Figure 3.4). Mixed thornveld had a more variable soil composition, as indicated by the two isolated points on the far right of the ordination diagram, which are higher in clay and silt content than the other points. The clusters of shrub mopane woodland and tall mopane woodland sites overlapped very little on the ordination diagram, with the shrub mopane woodland sites occurring at the lower side of the pH scale and the tall mopane woodland sites occurring at the higher end. The soil composition of the shrub mopane woodland sites was more sand dominated, while the tall mopane woodland sites had greater levels of silt and clay (Figure 3.4).

Table 3.3: PERMANOVA p-values of pairwise comparisons between the soil properties of the four vegetation management units; tall mopane woodland, shrub mopane woodland, mixed broadleaf woodland and mixed thornveld. Significant values in bold

Mixed broadleaf woodland				
Shrub mopane woodland	**0.001**			
Tall mopane woodland	**0.012**	**>0.001**		
Mixed thornveld	0.777	**0.004**	**0.008**	
	Mixed broadleaf woodland	Shrub mopane woodland	Tall mopane woodland	Mixed thornveld



(b)

Figure 3.4: PCA of soil characteristics for the vegetation management units; tall mopane woodland (♦), shrub mopane woodland (▼), mixed broadleaf woodland (+) and mixed thornveld (▲) showing (a) gradients of soil characteristics for topsoil pH (pH-T), subsoil pH (pH-S), topsoil clay content (Cl-T), subsoil clay content (Cl-S), topsoil silt content (Si-T), subsoil silt content (Si-S), topsoil sand content (Sa-T), subsoil sand content (Sa-S) and infiltration and (b) relationships between management units. Eigenvalues for axes one and two are 0.703 and 0.130 representing a cumulative variance of 83.3%.

3.2.6 Soil-Species relationships

Forward selection in a CCA found that both the sand-clay soil texture gradient ($p = 0.0001$) and the pH gradient ($p = 0.0318$) had a significant effect on tree species composition (Figure 3.5), while only the soil texture gradient had a significant effect on grass species composition (sand and infiltration $p = 0.0009$, clay and silt $p = 0.0009$) (Figure 3.6). All tree species occurring on the left of CCA axis 2 were found on soils which were sand dominated, while all species occurring on the right occurred on soils with high clay and silt content. *Terminalia sericea, Lonchocarpus nelsii* and *Acacia erioloba* occurred on acidic sandy soils, with *T. sericea* and *L. nelsii* occurring on soils with a greater sand content than *A. erioloba*. *Dichrostachys cinerea, Gymnosporia senegalensis, Ximenia americana* and *Rhus tenuinervis* occurred in sandy regions with a moderate pH, while *Combretum apiculatum, Grewia bicolour* and *Euclea divinorum* ordinate furthest along the pH gradient indicating that they were associated with moderately sandy, basic soils. *L. nelsii, T. sericea* and *A. erioloba* were found on more acidic, sandy soils. *Capparis tomentosa* and *Acacia tortilis* were associated with more acidic, clay and silt dominated soils, while *Colophospermum mopane, Grewia retinervis* and *Combretum imberbe* were found on the more basic, clay and silt dominated soils (Figure 3.5).

The grass species formed three groups distributed along the soil texture gradient. The first group was a tight cluster located slightly to the left of the centroid, closely associated with increasing sand content and comprised *Stipagrostis hirtigluma, Panicum maximum, Pogonarthria squarrosa, Dactylotenium gigantium* and *Digitaria eriantha*. The second group, *Urochloa mossambicensis, Chloris virgata, Sporobolus ioclados, Aristida meridionalis, Sporobolus fimbriatus, Enteropogon macrostachyus, Digitaria velutina* and *Cenchrus cilliaris*, was located slightly to the right and below the centroid and were found on a range of clay and silt dominated soils, while the third and smallest group comprised of *Eragrostis capensis, Heteropogon contortus, Panicum repens, Echinochloa colona* and *Acroceras macrum* was associated with soils with a high clay content (Figure 3.6).

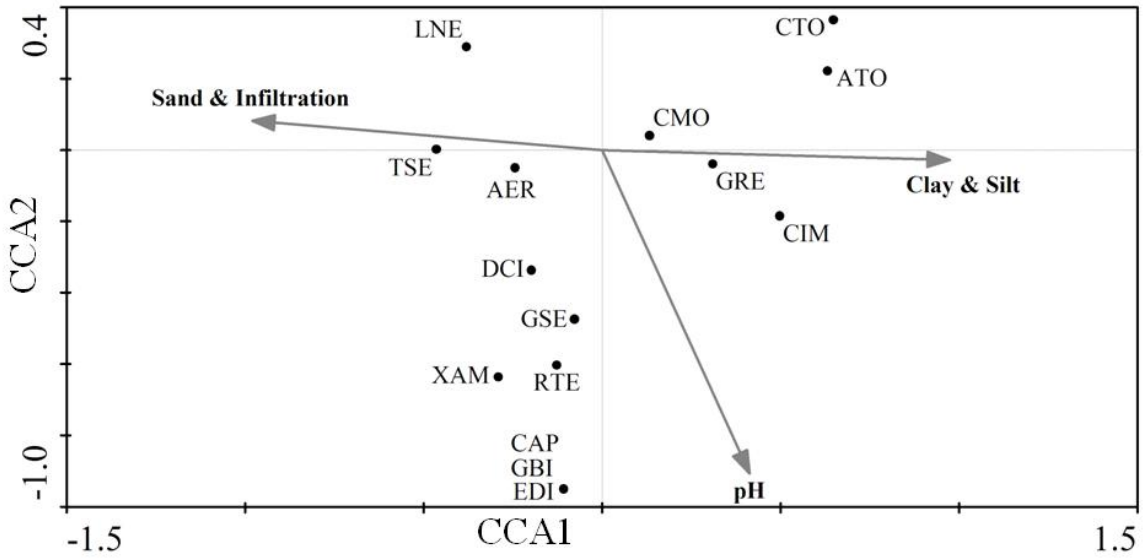


Figure 3.5: Plot of species and environmental variables along the first two axes of a canonical correspondence analysis (CCA) of tree species relative density and environmental data. The eigenvalues for axes one and two are 0.754 and 0.540 accounting for a cumulative variance of 82.5%. Sand & Infiltration account for 57% of the total variability ($p = 0.0001$), Clay & Silt for 55% ($p = 0.0001$) and pH for 29% ($p = 0.0318$). Species with less than 5% of their variance accounted for are not shown. Tree species abbreviations are explained in Appendix A.

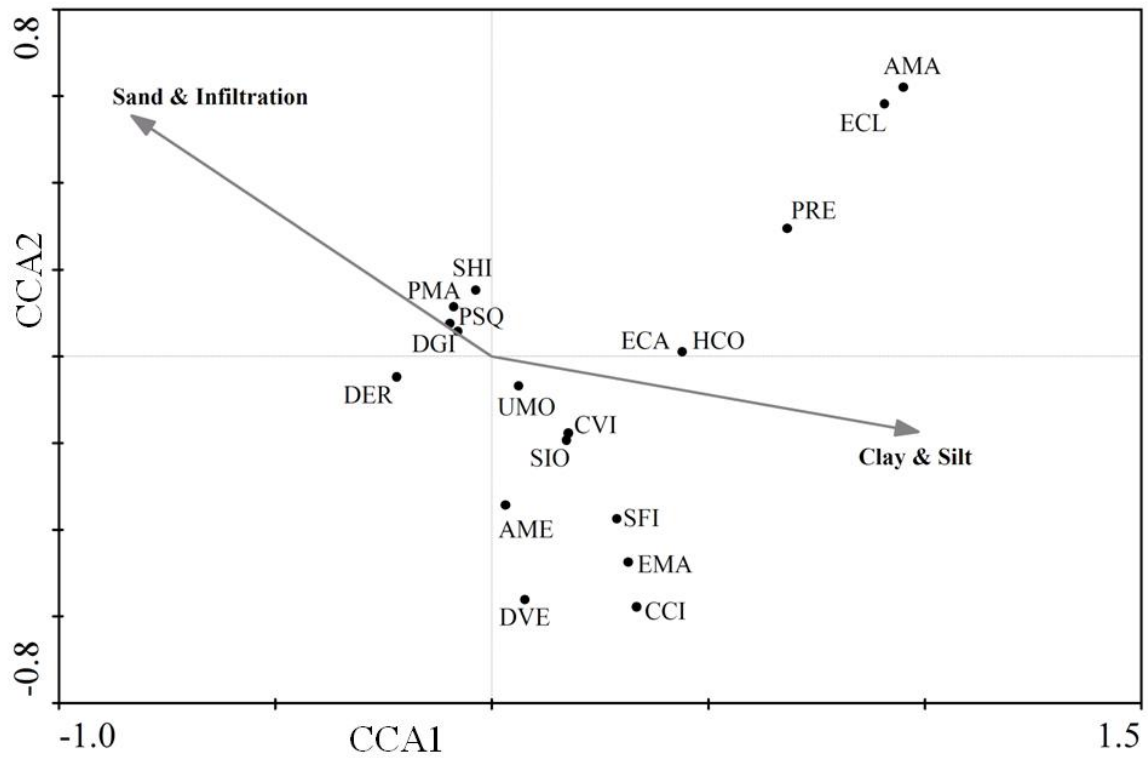


Figure 3.6: Plot of species and environmental variables along the first two axes of a canonical correspondence analysis (CCA) of grass cover and environmental data. The eigenvalues for axes one and two are 0.681 and 0.629 accounting for a cumulative variance of 100%. Sand & Infiltration account for 47% of the total variability (p = 0.0009) and Clay & Silt for 53% (p = 0.0003). The pH gradient was excluded as it did not have a significant effect on grass composition (p = 0.4742). Species with less than 5% of their variance accounted for are not shown. Grass species abbreviations explained in Appendix B.

3.4 DISCUSSION

The distribution of the vegetation management units indicates that the soils in NG33, the western and central regions of Moremi Game Reserve and the central and southern regions of NG34 are predominantly sandy, while the soils in north-eastern Moremi and eastern NG34 are more clay dominated.

Mixed thornveld has a variable distribution occurring mainly on basic sandy soils with some patches found on more acidic, clay dominated areas. As a result the species range from *A. erioloba* and *D. cinerea*, which thrive on deep, well-drained sands (Roodt 1998b), to clay-loving species such as *A. tortilis* (Roodt 1998b) and low densities of *C. mopane*. The grass layer is comprised of a mix of tall, tufted species such as *D. eriantha, D. gigantium* and *P. squarrosa*. Mixed broadleaf woodland favours similar

soil characteristics to the more sand dominated regions of mixed thornveld and as a result is generally closely associated with mixed thornveld occurring in patches within a thornveld matrix or between belts of thornveld and shrub mopane woodland. It is characterised by those broadleaf species, such as *L. nelsii* and *T. sericea*, which favour well-drained soils, although *C. mopane* does sometimes occur at low densities. It has a similar grass composition to mixed thornveld although the extent of the grass cover and the species composition may depend on the density of the woody vegetation.

The distribution of mixed thornveld and mixed broadleaf woodland is mainly limited to the western regions of Moremi Game Reserve, NG33 and NG34 parallel to the Gomoti River. This distribution correlates to the distribution of primary floodplains during the early 1900s (Johnson and Bannister 1977, McCarthy and Ellery 1994) when the Gomoti River was the major floodwater outflow to the south-eastern regions of the Okavango Delta (Bernard and Moetapele 2005). Decaying plant material and ash in the floodwaters releases cations, such as phosphorus, calcium, magnesium, potassium and sodium which when deposited into the floodplain soils would cause the increased pH levels still observed today (Bonyongo and Mubyana 2004).

Tall mopane woodland is dominant on the basic, clay-rich soils in north-east Moremi Game Reserve and eastern NG34. This vegetation is dominated by *C. mopane* with a sparse understory of *Grewia* species. The grasses are generally sparse as the woody cover is dense and the soils clay-dominated, allowing only shade-tolerant, hydrophilic species, such as *U. mossambicensis*, to survive. Shrub mopane woodland forms a transition zone of more acidic sandy soil between the thornveld dominated historic floodplains and the clay-rich tall mopane belt. It has a variable species composition with a range of species dominant in other vegetation management units occurring together.

The description and distribution of these four dry woodland and savanna vegetation management units differ greatly from those described by Mendelsohn and el Obeid (2004), with the mopane woodlands further divided by plant morphology into tall and shrub mopane, two growth forms which may indicate differences in underlying soil characteristics, fire regime or utilization (Lombard 2003, February et al. 2007), and the *Acacia* woodlands further divided into mixed thornveld and mixed broadleaf woodland. Jellema et al. (2002) divide the *Acacia* woodlands described by Mendelsohn and el Obeid (2004) into four groups while the mopane woodlands, which cover the entire south-eastern Delta region in the map produced by Mendelsohn and el Obeid (2004), remain as a single category, namely shrubbed woodland with mixed mopane (Jellema et al 2002). As can be seen from the vegetation units described in this chapter not only does the south-eastern Delta comprise of large areas of mixed thornveld not represented

by Mendelsohn and el Obeid (2004) or Jellema et al (2002), but there is a clear difference in terms of both species composition and soil characteristics between the stands of shrub mopane woodland described by Jellema et al (2002) and the stands of tall mopane woodland which cover large areas of Moremi Game Reserve and eastern NG34.

This study not only provides the essential base-line data and functional type classification to allow for the development of an effective adaptive management plan and monitoring program, but also augments understanding of species distribution in the southern Okavango Delta in terms of the underlying soil composition.

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CHAPTER 4: THE EFFECTS OF FIRE ON THE DRYLAND WOODY VEGETATION IN THE EASTERN OKAVANGO DELTA

4.1 INTRODUCTION

Fire is a common occurrence in savanna regions worldwide (Higgins et al. 2000). African communities have been burning grassland and savanna for as long as 55 000 years (Heinl et al. 2007). As a result burning is a powerful management tool which can be used to achieve numerous objectives such as; to remove the previous season's unpalatable growth and moribund material, to control woody encroaching plants, to provide out-of-season green forage, to reduce grass fuel loads and to improve grass cover for grazing and improved soil and water conservation (Trollope 1999, Goldammer and De Ronde 2004). In addition fire can be used to protect buildings from wildfires by burning firebreaks (Heinl 2005), to clear land in preparation for planting crops (Tlotlego 2004), to increase the availability of fish resources by both improving the accessibility of open water for fishing and increasing the availability of palatable shoots leading to an increase in the fish population by burning reed beds in the permanent and seasonal swamps (Cassidy 2003, Tlotlego 2004) and to improve the quality of harvested reeds and thatch grass by removing moribund material in swampy, wetland areas (Cassidy 2003).

The management of fire in Botswana is legislated by the Herbage Preservation Act of 1977. In addition to dictating the necessity of a burning permit which can only be obtained in Maun, the act states that it is illegal to burn land which you do not have legal rights over (Trollope et al. 2006). For this reason there is a widespread negative view of fire in Botswana. During the development of a fire management plan for the Okavango Delta Trollope et al. (2006) suggested several amendments to the Herbage Preservation Act which should assist in developing a more positive view of burning as a management tool and allow for greatly improved fire management. These amendments include the decentralisation of the District Fire Committee offices making permits more easily available, the introduction of a fire danger rating system dictating when it is safe to burn, mandatory assessment of the condition of the grass sward and an assessment of the fire-fighting equipment available to the manager conducting the burn (Trollope et al. 2006).

Coupled with this there is a need for an increase in fire ecology research in the Okavango Delta. Despite a relatively high fire frequency (Heinl et al. 2006) there is a lack of knowledge regarding the use of fire as a management tool in the area (DFRR 2011). Wild fires are perceived as undesirable in the Delta and are becoming increasingly frequent (Trollope et al. 2006). For this reason it was identified as one of the focal points for the vegetation resources component of the Okavango Delta Management Plan (ODMP) (DFRR 2011).

Since the ODMP was proposed in 2002 six postgraduate studies focussing on different aspects of fire ecology have been conducted, however much of this work is difficult to access, with theses only available in hardcopy and few resulting publications. Both Cassidy (2003) and Tlotlego (2004) worked in the northern panhandle region of the Okavango Delta. The ecology of this region is vastly different to that of the southern fan area encompassing the permanent and seasonal swamps. In the panhandle the Okavango river is contained between two steep skarps, resulting from parallel fault lines (Heinl et al. 2008), preventing the development of floodplains as observed further south in the Delta. Both of these studies focussed on the effects of fire on the local community. Cassidy (2003) examined the effects of fire on the availability of a number of resources, such as reeds, grazing land and abundance of fish using a combination of remote sensing to map burnt areas, vegetation sampling using transects and interviews with the local community. Fire frequency was found to be higher on the floodplains than near the main Panhandle channel and fire had less of an effect on access to resources than socioeconomic factors (Cassidy 2003). Tlotlego (2004) conducted a more focussed study examining the effects of burning on the availability of thatch grass using only remote sensing and interviews with the local community.

Banda (2004) worked in the southern Delta in the region of the Boro river investigating the effects of burning on soil micro-organisms by collecting soil samples in areas subjected to a management burn and similar unburnt areas. Fire was found to significantly alter the soil microbial community structure by increasing the fungal component and decreasing the bacterial component (Mubyana-John et al. 2007). Plasvic (2006a) investigated the effects of burning on the abundance of small mammals using box traps to capture animals in unburnt and recently burnt areas in Moremi Game Reserve. Burning was found to have a negative effect on the diversity of small rodents with all species leaving the burnt areas. Many of these species did not recolonise the area until several months after the fire, while some did not recolonise at all (Plasvic 2006b).

Both Tacheba (2002) and Heinl (2005) studied the effects of fire on vegetation. Tacheba (2002) focussed on the effect of season of burning on the species diversity and biomass of the vegetation on the seasonal floodplains of the southern Delta using remote sensing to map the burnt areas, floristic surveys and quadrat clipping for biomass measurements. It was found that no burning had not significantly affected vegetation structure, however greater biodiversity in burned areas was observed (Tacheba 2002). Further work has been conducted since this study linking the effects of fire on vegetation resources to local people's impressions of the government policy on burning in order to assist with the improvement of this policy (Tacheba et al. 2009). The work by Heinl (2005) investigated the effects resulting from the

interaction between fire and flooding on the seasonal floodplains of the southern Delta using remote sensing to map burning and flooding patterns and plots in which species abundance, cover and growth form were recorded. Fire frequency was found to affect cover of some wetland species, while most woody species were found to be negatively affected. Post-fire succession was not only driven by species specific life-history, but also by competition and niche differentiation (Heinl 2005). In addition to these a comprehensive fire management plan has been developed as part of the ODMP (Trollope et al. 2006).

While these studies have contributed greatly to the understanding of fire ecology in the Okavango Delta, little work has been conducted into the specific effects of burning on the dryland vegetation types surrounding the Okavango Delta. These dryland regions generally burn between May and October, with the northern *Burkea* woodlands burning more frequently than the mopane and *Acacia* woodlands in the south, as a result of low grass production in the southern regions (Trollope et al. 2006). While the effects of fire in the much dryland savanna regions of the Delta may be comparable to the effects observed in other semi-arid African savannas (Heinl 2005) this may not be the case in the dry sand veld mopane woodland. Trollope et al. (2006) note that wild fires in the mopane woodland regions of the south-eastern Delta had a negative effect on the herbaceous layer resulting in large patches devoid of vegetation and vulnerable to wind erosion. For this reason it is important to determine the effects of fire on the different types of dryland woody vegetation in the Okavango Delta.

The objectives of this chapter were to; (1) identify regions affected by a very hot fire in October 2008 by mapping the fire distribution from 2003, the earliest available images, to 2009 and (2) determine the influence of a single, widespread fire event on the vegetation characteristics of the four vegetation management units defined in chapter three, tall mopane woodland, shrub mopane woodland, mixed broadleaf woodland and mixed thornveld.

4.2 METHODS

4.2.1 Data Collection

4.2.1.1 Fire Mapping

In order to identify the regions affected by only the fire (FDI = 61 – 75) in October 2008 the fire distribution from 2003 – 2009 was mapped in ArcMap 10 (ESRI 2010) using active fire data downloaded from the University of Maryland's Fire Information for Resource Management System website (NASA/University-of-Maryland 2002, Davies et al. 2009). Of the sixteen long-term monitoring sites identified in each of these four management units, eight were located in areas burnt only in October 2008 and eight were located in areas which had not burnt since 2002 or earlier.

4.2.1.2 Vegetation

The methods used to sample the vegetation at each of these sites were a modified version of those used by Dahlberg (2000). At each of the sites three transects (100m by 3m) were set out approximately 5m apart in order to avoid overlap. GPS co-ordinates were recorded at the start and end points of each transect to allow for repeat sampling. The species and height class, <0.49m, 0.5-0.99m, 1-1.99m, 2-2.99m and >3m, of each woody plant rooted within the transect area was then recorded. The herbaceous layer was sampled using eleven 1m x 1m quadrats evenly spaced along the transect line. In each quadrat the percentage basal cover was recorded for each grass species. In addition the total percentage cover was recorded for other herbaceous species and bare ground. These herbaceous species were defined according to Roodt (1998b) as 'non-woody, seed bearing plants which die down to the ground after flowering'. Each species recorded in the herbaceous layer was then categorised as increaser 1, increaser 2, increaser 3 or decreaser according to ecological status as described in van Oudtshoorn (1999) and Camp and Hardy (1999). Increaser 1 species are abundant in underutilized veld, increaser 2 and increaser 3 species occur in overgrazed veld with increaser 3 species being more difficult to remove using grazing management as a result of their unpalatable nature. Decreasers are palatable species which decrease as a result of either under or over-utilization (Camp and Hardy 1999, van Oudtshoorn 1999). This sampling was conducted between February and April 2010.

4.2.1.3 Data Processing

The transect data were then used to calculate the density (individuals per hectare) of each tree species, each height class and total woody density. Tree species and height class data were also used to calculate the density of spizes which are pseudospecies created by dividing the density of each tree species into its height class components (Emslie and Adcock, 1994). This was done individually for each site. From this the following relative density datasets were developed; tree species composition, height class composition and spizes composition. In addition the following diversity indices were calculated for the woody component; Hill's N_1, Hill's N_2, Pielou's evenness and species richness (Begon et al. 2005). Hill's diversity indices N1 and N2 describe the diversity of abundant and very abundant species respectively, while Pielou's evenness co-efficient compliments the diversity indices, with values ranging from 0 to 1 and low values indicating that the species composition is dominated by certain species. The quadrat data were used to determine the average grass cover and composition for each site.

4.2.2 Data Analysis

4.2.2.1 Vegetation

Differences between the woody species composition, spizes composition, height class composition and grass cover between burnt and unburnt areas in each management unit were determined using analysis of similarities (ANOSIM) in PRIMER (Clarke and Gorley 2006). The factors contributing to those differences were determined using SIMPER in PRIMER (Clarke and Gorley 2006).

The effects of burning on total woody species density and the diversity indices; Hill's N_1, Hill's N_2, Pielou's evenness and species richness were determined using an independent 2-sample t-test in SPSS (IBM 2010). In order to meet the assumptions of the t-test the data for mixed broadleaf woodland Hill's N_1 were log transformed in Genstat (VSN-International 2009). The data for mixed broadleaf woodland tree density and shrub mopane woodland Hill's N_1 and Hill's N_2 were analysed using a Mann-Whitney U test in SPSS (IBM 2010) as the violations of the t-test assumptions could not be rectified using transformations.

4.3 RESULTS

4.3.1 Fire Mapping

The largest fire recorded in the seven year period between 2003 and 2009 took place in October 2008 and burnt approximately 80% of Ngamiland NG34 and the eastern half of NG33. This was the only burn that this region received during this period. Owing to the restrictions on burning in terms of the National Herbage Act it was not possible to conduct a controlled burning experiment, therefore this large, widespread burn provided the opportunity to conduct this study. All the burnt sites were located within NG33 and NG34, while the unburnt sites are located mainly in the western section of NG33 and central Moremi Game Reserve with a small number in the unburnt eastern region of NG34. These areas are adjacent to one another and thus receive similar rainfall and have similar underlying soil types. These areas are all exclusively utilized by wildlife and there are no fences separating these areas so there are few differences in terms of animal numbers, type and movement.

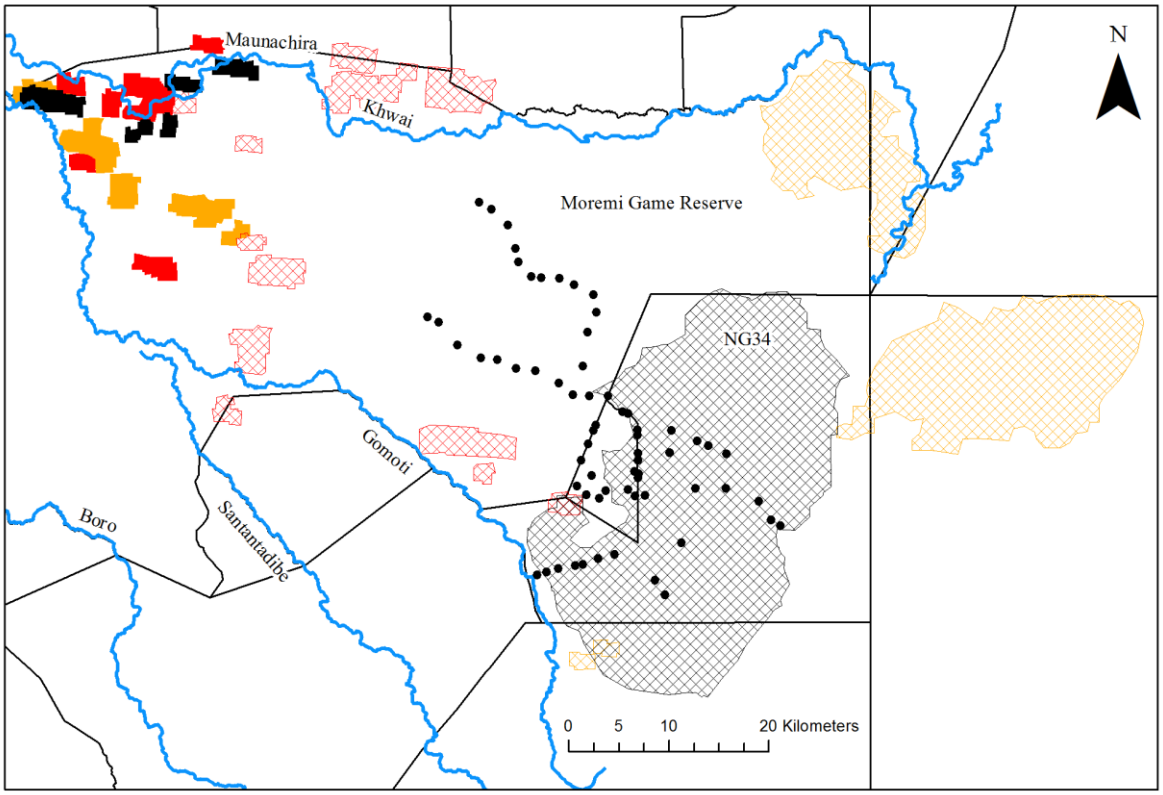

Figure 4.1: Distribution of fires in NG33, NG34 and Moremi Game Reserve from 2003 to 2009. Fires for 2003 (solid black), 2004 (solid red), 2005 (solid orange), 2006 (hatched orange), 2007 (hatched red), 2008 (hatched black). No fires were recorded in 2009. Sample sites indicated by solid black symbols.

4.3.1 Influence of burning on VMUs

Burning in mixed broadleaf woodland had a significant effect on all factors except height class. There was however a significant effect on spizes indicating that the burn may have affected height distribution of specific species but not affected the general height distribution of the population (Table 4.1). Both tree species composition and grass cover were affected by burning in shrub mopane woodland, while only tree species composition was affected in tall mopane woodland. All factors recorded were affected by the burn in mixed thornveld (Table 4.1).

Table 4.1: ANOSIM analysis on the relative density of tree species composition, spizes composition and height class composition, and sward compositional cover between burnt and unburnt areas in four vegetation management units. Significant values in bold

	p-value			
	Tree species	Spizes	Height class	Sward cover
Mixed broadleaf woodland	**0.009**	**0.019**	0.134	**0.004**
Shrub mopane woodland	**0.073**	0.107	0.296	**0.001**
Tall mopane woodland	**0.015**	0.125	0.250	0.131
Mixed thornveld	**0.016**	**0.028**	**0.009**	**0.018**

The significant difference between tree species composition in burnt and unburnt mixed broadleaf woodland (Table 4.1) is largely due to the relative density of *Croton megalobotrys* which in the unburnt sites is double that of the burnt sites (Table 4.2). The relative density of *Lonchocarpus capassa* in the unburnt sites is also double that occurring in the burnt sites, while *Diospyros lycioides* is four times more abundant in the burnt sites. *Lonchocarpus nelsii* is eight times and *Acacia erioloba* twice as abundant in the burnt sites. *Grewia flavescens* and *Dichrostachys cinerea* have a mean relative abundance of 13% and 5% in the burnt sites but do not occur at all in the unburnt sites (Table 4.2).

Croton megalobotrys also contributes to the significant difference between the burnt and unburnt sites in terms of spizes (Table 4.1), with the unburnt sites having a relative density of 42% and the burnt sites a relative density of 17% of *C. megalobotrys* taller than 3m. Burning was also found to affect the sward cover and composition in mixed broadleaf woodland (Table 4.1). Herbaceous cover increased by 14% and a small increase in bare ground was also observed with burning (Table 4.3). The four dominant grass species, *Urochloa mossambicensis, Eragrostis lehmanniana, Cynodon dactylon* and *Chloris virgata* all decreased in abundance with burning, while *Panicum maximum* abundance increased slightly (Table 4.3).

The significant difference between the woody species composition of burnt and unburnt shrub mopane woodland (Table 4.1) can be mainly attributed to *L. nelsii* and *C. mopane*. The unburnt sites had more than double the relative density of *L. nelsii* and a greater relative density of *C. mopane* than the burnt sites. The burnt sites did however have five times more *A. erioloba* than the unburnt sites and had relative densities greater than 5% of *L. capassa*, *Combretum hereroense* and *Terminalia sericea*, all of which were absent in the unburnt sites (Table 4.2).

Burning in shrub mopane woodland also resulted in a significant (Table.4.1) decrease (30%) in the proportion of bare ground present (Table 4.3). The majority of this bare ground appeared to be covered by herbaceous species as the herbaceous cover increased by 19%. Burning also resulted in an increase in the abundance of *U. mossambicensis* and *E. lehmanniana* (Table.4.3).

Only tree species composition in tall mopane woodland was affected by burning (Table 4.1). There was a slight decrease in the relative density of *D. cinerea* and *Grewia retinervis* was completely absent in the burnt sites. The relative density of *C. mopane* increased in the burnt sites in tall mopane woodland and mixed thornveld but this was possibly as a result of the decrease in the two understory species (Table 4.2).

The main difference between the woody species composition in burnt and unburnt mixed thornveld is a substantially greater relative density of *A. erioloba* in the burnt sites. *C. mopane* and *Combretum imberbe* also had a greater relative density in the burnt sites, while *D. cinerea*, *Acacia nigrescens* and *Acacia tortilis* were all present in the unburnt sites but not in the burnt sites (Table 4.2).

The difference in *A. erioloba* relative density between burnt and unburnt mixed thornveld was largely due to the difference in relative density of *A. erioloba* taller than 3m and shorter than 0.5m. In the burnt sites 51% of the woody cover comprises of *A. erioloba* taller than 3m, while the same height class in the unburnt sites contributes only 16%. The opposite is true for *A. erioloba* shorter than 0.5m with a relative density of 25% in the unburnt sites and 11% in the burnt sites.

These differences in structural composition between burnt and unburnt mixed thornveld can be seen as a general trend not restricted to *A. erioloba*. The burnt sites had 53% of the woody layer taller than 3m and only 14% shorter than 0.5m, while the unburnt sites had only 20% taller than 3m but 47% shorter than 0.5m. The unburnt sites also had a greater proportion of woody species in the 1-1.99m height class (16% in the burnt sites and 19% in the unburnt sites) while the burnt sites had a greater proportion of woody species in the 2-2.99m height class (12% in the burnt sites and 5% in the unburnt sites).

The fire in mixed thornveld resulted in a significant increase (Table. 4.1) in the extent of bare ground and cover of *Digitaria eriantha* (Table 4.3), but a decrease in the cover of herbaceous plants, *U. mossambicensis*, *E. lehmanniana*, *C. dactylon* and *Eragrostis rigidior* (Table 4.3).

Table 4.2: Mean relative density of tree species composition contributing to the dissimilarity between burnt and unburnt areas in four vegetation management units from SIMPER analysis. Species in shaded blocks contribute more than 5% and species in bold more than 20% to the dissimilarity between burnt and unburnt sites. Tree species abbreviations explained in Appendix A

	Mixed broadleaf woodland		Shrub mopane woodland		Tall mopane woodland		Mixed thornveld	
	Burnt	Unburnt	Burnt	Unburnt	Burnt	Unburnt	Burnt	Unburnt
AER	7	4	10	1	1	0	**83**	**55**
ANI	3	0	0	0	0	0	0	8
ATO	0	0	0	0	0	0	0	18
BAL	5	0	0	0	0	0	0	0
CHE	0	0	7	0	0	0	0	0
CIM	0	0	0	0	0	0	5	4
CME	**28**	**61**	0	0	0	0	0	0
CMO	2	4	**44**	**61**	**94**	**87**	7	1
DCI	5	0	0	0	1	2	0	8
DLY	2	8	0	0	0	0	0	0
GFA	0	0	4	0	0	0	0	0
GFS	13	0	0	0	0	0	0	0
GRE	0	3	0	0	**0**	**11**	0	0
LCA	6	14	7	0	0	0	0	0
LNE	17	2	**14**	**35**	0	0	0	0
RTE	4	0	0	0	0	0	0	0
TSE	0	0	6	0	1	0	0	0
ZMU	0	0	0	0	0	0	2	2

Table 4.3: Mean cover of grass species (with ecological status in brackets – I1 = Increaser 1, I2 = Increaser 2, I3 = Increaser 3, D = Decreaser) contributing to the dissimilarity between in burnt and unburnt areas in four vegetation management units from SIMPER analysis. Species in shaded blocks contribute more than 5% and species in bold more than 20% to the dissimilarity between burnt and unburnt sites. Grass species abbreviations are explained in Appendix A.

	Mixed broadleaf woodland		Shrub mopane woodland		Tall mopane woodland		Mixed thornveld	
	Burnt	Unburnt	Burnt	Unburnt	Burnt	Unburnt	Burnt	Unburnt
AJU (I3)	0	0	1	4	1	14	0	0
Bare ground	49	37	**56**	**86**	73	67	53	35
CDA (I2)	0	7	2	0	0	0	1	9
CVI (I2)	1	7	0	0	0	0	0	0
DER (D)	0	0	2	0	2	0	**21**	**11**
ELE (I2)	6	14	5	3	4	2	5	14
ERG (I2)	0	0	0	0	3	0	1	5
HERB (I1)	**24**	**10**	**21**	**2**	5	5	**7**	**11**
PMA (D)	3	1	0	0	0	0	3	1
SFI (I2)	0	0	0	0	0	1	0	0
SVE (I2)	0	2	0	0	0	0	0	0
UMO (I2)	14	17	7	1	7	8	2	9

Burning had no effect on Hill's N1 or Hill's N2 in any of the four vegetation management units and thus did not alter the diversity of the abundant or very abundant species in any of the vegetation management units (Table 4.4). Pielou's evenness was affected only in tall mopane woodland with the burnt areas having an evenness coefficient of 0.06 and the unburnt areas having an evenness coefficient of 0.15 (Table 4.4 and Table 4.5). This indicates that the unburnt areas have a greater number of dominant species than the burnt areas. This is supported by the tree species abundance data which indicate that unburnt tall mopane woodland is dominated by both *C. mopane* and *G. retinervis* while the burnt areas are dominated by *C. mopane* alone (Table 4.2).

Mean species richness was affected in both shrub mopane woodland and mixed thornveld (Table 4.4). In shrub mopane woodland burning resulted in an increase in mean species richness, while in mixed thornveld burning decreased mean species richness (Table 4.5). Total woody species density was only affected by burning in mixed broadleaf woodland (Table. 4.4) with burnt areas having a much greater total woody species density than unburnt areas (Table 4.5). This large difference may

be as a result of a post-burn germination flush as the SIMPER analysis on the relative density of spizes showed the burnt regions to have a greater number of species represented in the > 0.5m height class than the unburnt regions.

Table 4.4: P-values of two-sample t-test between burnt and unburnt areas in four vegetation management units. Data for mixed broadleaf woodland Hill's N1were log transformed. Data for mixed broadleaf woodland total woody species density and shrub mopane woodland Hill's N_1 and Hill's N_2 were analysed using Mann-Whitney U test. Significant vales in bold

	Hills's N_1	Hills's N_2	Evenness	Richness	Density
Mixed broadleaf woodland	0.132	0.204	0.354	0.300	**0.010**
Shrub mopane woodland	0.227	0.462	0.409	**0.005**	0.447
Tall mopane woodland	0.186	0.270	**0.032**	0.382	0.658
Mixed thornveld	0.052	0.270	0.205	**0.035**	0.851

Table 4.5: Data means (±SE) for Hill's N_1, Hill's N_2, Pielou's evenness, species richness and total woody species density in burnt and unburnt area in four vegetation management units

	Hill's N_1		Hill's N_2		Pielou's evenness		Species richness		Total tree species density	
	Burnt	Unburnt	Burnt	Unburnt	Burnt	Unburnt	Burnt	Unburnt	Burnt	Unburnt
Mixed broadleaf woodland	4.5 ± 0.92	2.5 ± 0.31	3.8 ± 0.81	2.6 ± 0.48	0.2 ± 0.02	0.2 ± 0.03	3.6 ± 0.53	7.3 ± 1.40	1097.9 ± 213.36	283.3 ± 29.04
Shrub mopane woodland	3.2 ± 0.62	1.9 ± 0.13	2.7 ± 0.58	1.8 ± 0.15	0.2 ± 0.02	0.2 ± 0.04	3.4 ± 0.32	5.8 ± 0.65	1408.3 ± 240.31	1795.8 ± 432.83
Tall mopane woodland	1.3 ± 0.07	1.5 ± 0.15	1.2 ± 0.06	1.4 ± 0.16	0.1 ± 0.02	0.2 ± 0.03	2.6 ± 0.24	3.3 ± 0.77	2304.2 ± 705.73	2703.7 ± 552.21
Mixed thornveld	1.5 ± 0.25	2.3 ± 0.25	1.6 ± 0.52	2.3 ± 0.31	0.1 ± 0.05	0.2 ± 0.03	3.8 ± 0.56	2.0 ± 0.56	204.2 ± 87.10	222.9 ± 45.20

4.4 DISCUSSION

Contrary to the observations by Heinl (2005) the different types of dryland vegetation respond differently to burning. Mixed thornveld was the most significantly affected with all four aspects of structure and composition affected, followed by mixed broadleaf woodland, shrub mopane woodland and finally tall mopane woodland. Both mixed thornveld and mixed broadleaf woodland have extensive grass cover providing a substantial fuel load and resulting in a more intense fire than would be experienced in shrub mopane woodland and tall mopane woodland. The woody species most affected by burning were *Acacia erioloba* in mixed thornveld, *Croton megalobotrys* in mixed broadleaf, *Colophospermum mopane* in shrub mopane woodland and *Grewia retinervis* in tall mopane woodland.

As expected the cover of small *A. erioloba* (<0.5m) decreased substantially as a result of burning. These plants are within the zone of most intense heat and thus experience high fire induced mortality, while those specimens taller than 2m do not and thus dominate the burnt areas. It is generally accepted that these taller specimens survive as a result of the elevation of the apical buds (Balfour and Midgley 2006), however this may not be applicable in this case as *A. erioloba* is a slow-growing species (Venter and Venter 2002). As the species is intolerant of fire (Seymour and Huyser 2008) one would expect to see rapid stem elongation in order to escape the zone of most intense heat, however the species does not grow more than 500mm per year under optimum conditions (Venter and Venter 2002). Being an arid zone species this rapid stem elongation is less important than for mesic savanna species as fires are not as frequent (Seymour and Huyser 2008). In the early growth stages *A. erioloba* develops a long tap root with an extensive root system (Smit 1999, Venter and Venter 2002) rather than allocating resources to stem elongation. The seedlings also appear to allocate more resources to stem thickening than their mesic savanna counterparts (pers. obs.) as this contributes substantially to the fire survival of those individuals which grow to maturity (Balfour and Midgley 2006). The thicker the stem of the plant the lower the level of heat induced damage to the xylem and the greater the chance of survival (Balfour and Midgley 2006). This may also explain the dramatic decrease in *C. megalobotrys* density after burning, despite the majority of the plants being taller than 3m. *Croton megalobotrys* is a multi-stemmed species with a rapid growth rate (1500mm p.a.) (Roodt 1998a, Venter and Venter 2002). The wood is light and burns quickly (Roodt 1998a). The species has a slender trunk (Grant and Thomas 2005) as rapid growth does not allow for stem thickening. This coupled with the flammable nature of the wood results in high levels of fire-induced mortality. As *C. megalobotrys* is a shady species with large leaves, the removal of these plants increases the available light, allowing for a germination flush as reflected by the large number of species represented in the <0.5m class.

Despite *C. mopane* being sensitive to fire (Roodt 1998a), a far greater mortality was observed in shrub mopane woodland than in tall mopane woodland. This can be attributed to the difference in species growth form between these two vegetation management units. Tall mopane occurs on clay dominated soils which hold more moisture and are more nutrient rich. This allows the young *C. mopane* to quickly grow into tall, single stemmed trees with stems thick enough to tolerate burning and a canopy beyond the reach of browsers and fire (Roodt 1998a, Balfour and Midgley 2006, February et al. 2007). The sand dominated soils underlying shrub mopane woodland are drier and nutrient poor preventing this rapid growth and resulting in a short, multi-stemmed shrubby growth form, vulnerable to fire and browsing (Roodt 1998a, February et al. 2007). Despite having no effect on the tall, single-stemmed *C. mopane* in tall mopane woodland, burning completely removed the dominant understory species, *Grewia retinervis*. This species has a similar structure to *C. megalobotrys*, with multiple stems and light wood, and was thus negatively affected by burning despite the majority of individuals being taller than 1m.

The fire took place in October 2008 which is early summer in the Okavango Delta, after the growing season has commenced. Early summer burns have been observed to move slower than late winter fires, damaging the grasses which are no longer dormant and exposing the shoot apices to temperatures above the critical level for extended time periods (Trollope 1987). Contrary to the observations of Trollope et al (2006) burning significantly affected the grass species composition and cover in all vegetation management units except tall mopane woodland. This may be due to the fact that tall mopane woodland is dominated by tall, shady *C. mopane* and thus had very little grass or herbaceous cover in the unburnt areas. The majority of the grass species affected by the burn were increaser two species which are abundant in over-utilized veld (van Oudtshoorn 1999). The only increaser three species affected by burning was *Aristida junciformis*, also commonly found in overgrazed veld (van Oudtshoorn 1999). It was affected only in shrub mopane woodland where burning decreased cover. Burning increased bare ground and decreased the cover of all increaser two grasses in both mixed broadleaf woodland and mixed thornveld. *Panicum maximum* was the only decreaser species affected by burning in mixed broadleaf woodland while both *P. maximum* and *Digitaria eriantha* were affected in mixed thornveld, with the cover of *P. maximum* increasing slightly and the cover of *D. eriantha* increasing substantially. It is unlikely that burning alone is responsible for the decrease in cover of the increaser two species but rather a combination of burning and grazing as wildlife, particularly warthog, impala, zebra and wildebeest, are drawn to newly burnt areas to graze the highly palatable new growth (Grossman et al. 1999). Many of the increaser two species, particularly *Eragrostis lehmanniana* and *Urochloa mossambicensis*, are unable to

withstand heavy grazing in the early growth stages (Chippindall and Crook 1976, van Oudtshoorn 1999) and are outcompeted by the grazing tolerant decreaser species, such as *D. eriantha* (van Oudtshoorn 1999). The herbaceous cover in mixed broadleaf woodland and mixed thornveld responded differently to burning with mixed broadleaf woodland showing a substantial increase in herbaceous cover and mixed thornveld showing a slight decrease. As observed in mixed broadleaf woodland, shrub mopane woodland also showed a substantial increase in herbaceous cover and a slight increase in decreaser species, but a decrease in the amount of bare ground. This may be due to the fact that long to medium grass feeders, such as buffalo, select for the dense, woody, undergrazed regions, such as shrub mopane woodland and tall mopane woodland (personal observation), to avoid competition with the short grass feeders concentrated in regions such as mixed broadleaf woodland and mixed thornveld (Grossman et al. 1999). These long to medium grass feeders are unable to utilize the new growth on the burnt grass sward allowing the increaser two species to spread.

Of the various management objectives set out to be achieved by burning; to remove the previous season's unpalatable growth, to control encroaching plants, to provide out-of-season green forage, to reduce grass fuel loads and to improve grass cover for grazing and improved soil and water conservation (Trollope 1999, Goldammer and De Ronde 2004) not all are applicable to the Okavango Delta. The network of rivers extending from the seasonal and permanent swamp regions into the southern dry woodland regions result in an associated network of floodplains which remain green during the dry season, functioning as key forage resources for grazing herbivores. Although the floodwaters arrive in April, the floodplains remain inundated until September resulting in these areas not only providing forage resources but also available surface water during the dry season (McCarthy et al. 2003). As there are no fences around individual concession areas and wildlife reserves north of the southern buffalo fence the wildlife is also free to move further north into the seasonal swamp regions if forage becomes limited. For these reasons there is no need to burn in order to provide out-of-season green forage. In addition the Okavango Delta has a very low elevation (McCarthy and Ellery 1998) resulting in little erosion in the dry woodland regions and negating the need for burning in order to promote soil conservation.

Management burning in order to remove moribund material and to reduce grass fuel loads is only applicable in mixed thornveld and mixed broadleaf woodland as both of these vegetation management units have greater than 60% grass cover in their moribund state, while shrub mopane woodland and tall mopane woodland have less than 40%. This burning can however have a detrimental effect by reducing the forage yield in the season following the burn as some of the growing points are damaged and take

time to be replaced (Trollope 1999). For this reason burning should be conducted while the plants are still dormant in order to reduce the level of damage to the growing points. This burning also improves the species composition of the sward by increasing the cover of palatable decreaser species and decreasing the cover of increaser two and three species. Burning in mixed thornveld and mixed broadleaf woodland also affected the woody layer with mixed thornveld showing a marked decrease in short, woody plants, while in mixed broadleaf woodland the density of tall, multi-stemmed species decreased. Burning is thus an effective method of reducing the density of encroaching woody species in mixed thornveld but not in mixed broadleaf woodland as the resources made available by the removal of the tall, multi-stemmed species facilitated an increase in seedling density. Shrub mopane woodland was the only vegetation management unit where burning resulted in an increase in grass cover, however the cover of other herbaceous species also increased substantially. As these herbaceous species die after seeding (Roodt 1998b) a considerable increase in bare ground will be observed in the dry season. In addition burning in shrub mopane woodland will perpetuate the development of the multi-stemmed shrub mopane growth form (Lombard 2003) by encouraging coppice growth (Goldammer and De Ronde 2004) and as a result increasing bush thickening and making the area less accessible to wildlife. The only effect of burning in tall mopane woodland was to remove the scattering of multi-stemmed understory species.

4.5 CONCLUSION

Burning in shrub mopane woodland and tall mopane woodland should be discouraged due to the negative effects observed, while burning in mixed thornveld and mixed broadleaf woodland may be effective in achieving some management objectives, such as decreasing grass fuel loads, removing unpalatable growth, improving sward species composition and, in the case of mixed thornveld, reducing the density of encroaching species, provided that the frequency and season of burning are carefully monitored.

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CHAPTER 5: THE EFFECTS OF WILDLIFE AND LIVESTOCK UTILIZATION ON SHRUB MOPANE WOODLAND AND MIXED THORNVELD

5.1 INTRODUCTION

Of the tribes who migrated to the Okavango Delta approximately 250 years ago, all except the San and the Baswara kept some form of livestock (Campbell 1976, Darkoh and Mbaiwa 2009a). The Batwana, Ovaherero, Bagwato and Bayei kept cattle, while the Bakalagadi were more focused on small stock, keeping goats and sheep (Campbell 1976, Bailey 1998). As a result the vegetation evolved under light and intermittent utilization by wildlife and the livestock belonging to nomadic tribesmen. As the population increased and developed a less nomadic, more modern lifestyle the number of livestock increased accordingly and the grazing areas became restricted to areas close to settlements (Kelley and Walker 1976). In the last two decades the importance of livestock production has been further emphasised by the Rural Development Programme which encouraged and assisted non-farming ethnic groups, such as the Baswara to become involved in both crop and livestock farming (Darkoh and Mbaiwa 2009a). In addition to traditional livestock farming, commercial livestock farming is of great value to the Botswana economy.

During the 1970s in order to meet the European union export requirements that livestock not come into contact with wildlife, numerous veterinary cordon fences were built around the Okavango Delta (Bailey 1998) preventing the wildlife from utilizing the grazing areas outside the Delta which had previously been the case. Rather than negatively affecting the wildlife, as other veterinary cordon fences in central and eastern Botswana had done (Hannah et al. 1988), the fences around the Delta, coupled with the presence of the Trypanosomiasis carrying Tsetse fly, and foot and mouth carrying Buffalo, preserved the Okavango Delta and large portions of land to the east of it for the exclusive use of wildlife (Ross 1987). An estimated 48.8% of the Okavango Delta Ramsar site falls under community ownership (Trollope et al. 2006) and despite leasing the majority of the land for hunting and photographic tourism purposes many communities still live inside the veterinary cordon fence. Although the Okavango Delta and some regions to the east have been declared a cattle-free zone (Ross 1987, Jansen and Madzwamuse 2003) human settlement is still allowed on the outer edges of the Delta (Darkoh and Mbaiwa 2009b) and some communities still keep goats and donkeys within the Wildlife Management Area. The national wetlands policy and strategy developed in 1999 stated that one of the major causes of loss of biodiversity in the Okavango Delta is overgrazing and changing land use (Jansen and Madzwamuse 2003). For this reason emphasis has been placed on the importance of monitoring the effects of different forms of land use on vegetation (Ringrose et al. 2003).

The objective of this chapter was to determine the effects of the three different forms of herbivore utilization (Wildlife vs. Cattle & Goats vs. Goats only) on the woody layer species composition and structure and the grass sward species composition and cover in shrub mopane woodland and mixed thornveld.

5.2 METHODS

5.2.1 Data Collection

5.2.1.1 Experimental design

This study was conducted at three locations in the south-eastern Okavango Delta with different forms of land utilization. Areas utilized exclusively by wildlife were sampled within Ngamiland NG33, NG34 and Moremi Game Reserve in the wildlife management area inside the veterinary cordon fence. Areas utilized by small stock only were sampled within the grazing areas around Sankuyo village inside the veterinary cordon fence, while areas utilized by cattle and small stock were sampled in and around Shorobe village. Sankuyo village is the only settlement in NG33 and NG34 and has a population of approximately 400 (Mazizi-Resources-Pty-Ltd 2009, CSO 2011). The community is involved in the community based natural resource management programme and generate income by leasing the land in NG33 and NG34 to tourism and hunting operators and allowing the development of tourist and research camps within the lease area. Many of these operators and camps employ people from the village and some 50 people also work for the Sankuyo Tshwarangano Management Trust which oversees the leasing of land and management of NG33 and NG34 (Mbaiwa 2004). These activities are the major source of income for the community however they still keep a small stock of goats and donkeys in the areas close to the village.

The village of Shorobe is located south of the veterinary cordon fence outside the wildlife management area. Livestock farming is one of the main sources of income for the community and approximately 65% of households in the Shorobe area own some form of livestock (Darkoh and Mbaiwa 2009b). The village itself has a population of approximately 1000, while the greater Shorobe area is home to an additional 2000 people (CSO 2011). The community keeps cattle, donkeys and goats. Although the Botswana government conducts agricultural surveys the focus is on the number of households owning stock and the productivity of that stock, rather than the number of animals per unit area. These results are also presented in a fairly general format using geographic regions such as Ngamiland East for the region encompassing Shorobe which makes it impossible to calculate the current carrying capacity of the area. The most recent survey, conducted in 2004, estimates Ngamiland East to have a cattle population of approximately 111 273 and a goat population of approximately 138 509 (CSO 2011). No information on livestock numbers is available for the Sankuyo region as the survey does not include villages in the wildlife management area.

The experimental design comprised of seventy non-replicated, spatially independent sites located within three areas under different management practices (Davies et al. 2006, Holmes 2007, Cleary et al. 2010). Eight of the sites were located in the grazing areas surrounding Sankuyo, thirty in Shorobe and thirty-two in the wildlife management area.

A Sankuyo (SAN) is located within the wildlife management area, livestock grazing is restricted to the areas within and immediately adjacent to the village in order to minimise the loss of livestock to predators. Consequently the number of sample sites in Sankuyo was limited to eight and these were located fairly close to one another. Sankuyo and the adjacent grazing areas are located in the vegetation management unit, shrub mopane woodland (Figure 5.1).

Shorobe (SHO) is located south of the veterinary cordon fence and therefore does not have the predator related restrictions on grazing areas experienced by livestock owners in Sankuyo. Shorobe covers a substantially larger area than Sankuyo and has a population approximately four times larger and thus would be expected to have a greater number of livestock. The grazing areas in Shorobe fall under shrub mopane woodland in the east and mixed thornveld in the west. Of the thirty sites sampled in Shorobe, eighteen were located in shrub mopane woodland and twelve in mixed thornveld (Figure 5.1).

Within the wildlife management area (WMA) thirty-two sites were sampled, sixteen sites in shrub mopane woodland and sixteen in mixed thornveld. These sites were widely scattered across NG33, NG34 and Moremi Game Reserve (Figure 5.1).

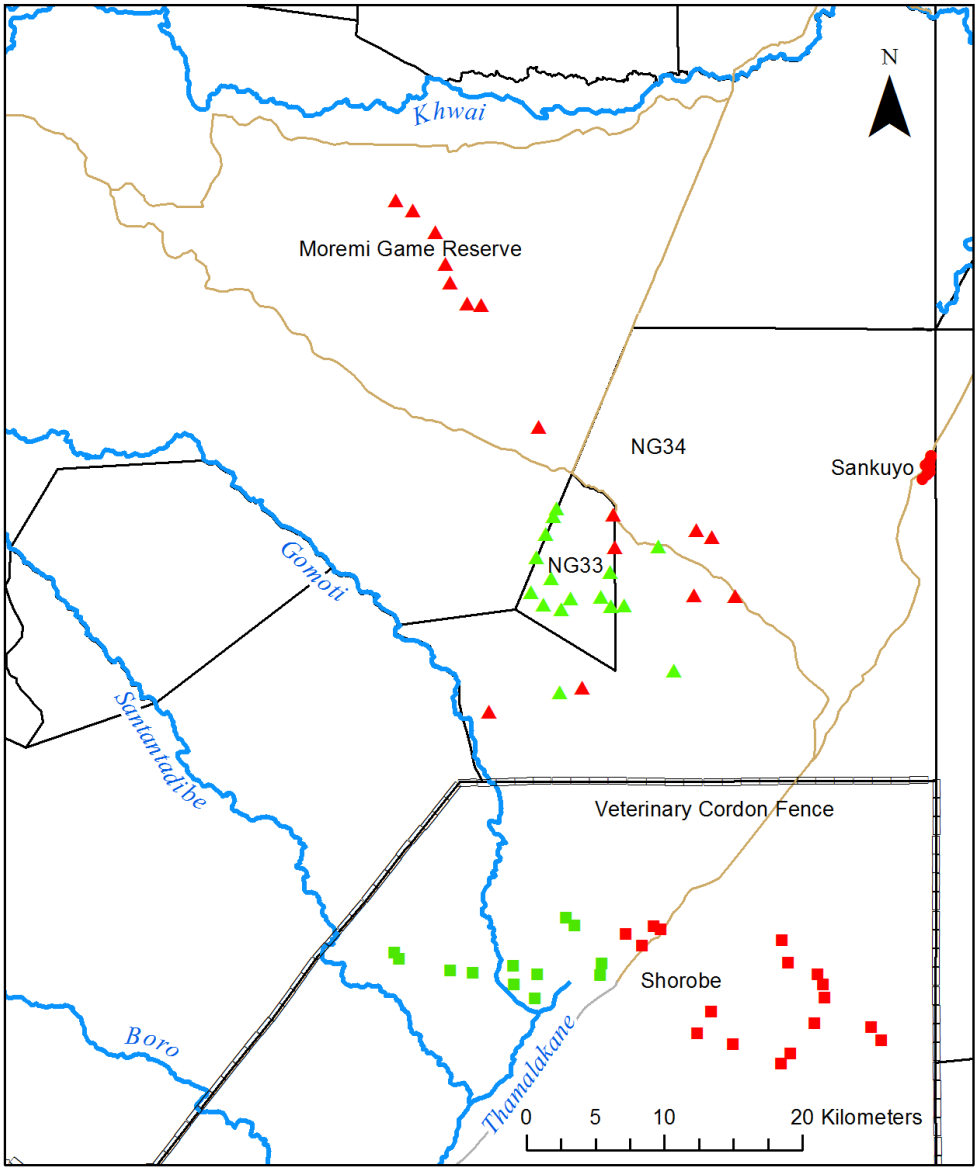

Figure 5.1: Geographic locations of sample sites for shrub mopane woodland (red) and mixed thornveld (green) in the wildlife management areas (triangles), Shorobe (squares) and Sankuyo (circles). Tarred roads are indicated in grey and dirt roads in brown.

5.2.1.2 Vegetation

The field sampling methods used were a modified version of those described by Dahlberg (2000). At each of the sample sites three transects (100m by 3m) were set out approximately 5m apart to prevent overlap of sampling area. GPS co-ordinates were recorded at the start and end points of each transect to allow for repeat sampling. The species and height class, <0.49m, 0.5-0.99m, 1-1.99m, 2-2.33m and >3m, of each woody plant rooted within the transect area was then recorded. The herbaceous layer was sampled using

eleven 1m x 1m quadrats evenly spaced along the transect line. In each quadrat, the percentage basal cover was recorded for each grass species. In addition the total percentage cover was recorded for herbaceous species and bare ground. Herbaceous species were defined according to Roodt (1998b) as 'non-woody, seed bearing plants which die down to the ground after flowering'. Each species recorded in the herbaceous layer was then categorised as increaser 1, increaser 2, increaser 3 or decreaser according to ecological status as described by van Oudtshoorn (1999) and Camp and Hardy (1999). Increaser 1 species are abundant in underutilized veld, increaser 2 and increaser 3 species occur in overgrazed veld with increaser 3 species being more difficult to remove using grazing management as a result of their unpalatable nature. Decreasers are palatable species which decrease as a result of either under or over-utilization (Camp and Hardy 1999, van Oudtshoorn 1999).

5.2.1.3 Data Processing

The transect data were then used to calculate the density (individuals per hectare) of each tree species, each height class and total woody density. Tree species and height class data were also used to calculate the density of spizes which are pseudospecies created by dividing the density of each tree species into its height class components (Emslie and Adcock 1994). This was done individually for each site. From this the following relative density datasets were developed; woody species composition, height class composition and spizes composition. In addition the following diversity indices were calculated for the woody component; Hill's N_1, Hill's N_2, Pielou's evenness and species richness (Begon et al. 2005). Hill's diversity indices N1 and N2 describe the diversity of abundant and very abundant species respectively, while Pielou's evenness co-efficient complements these diversity indices with values ranging from 0 to 1 and low values indicating that the species composition is dominated by certain species (Begon et al. 2005). The quadrat data were used to determine the average grass cover and composition for each site.

5.2.2 Data Analysis

5.2.2.1 Vegetation

Differences between the tree species composition, spizes composition, height class composition and grass cover between different forms of utilization in shrub mopane woodland and mixed thornveld were determined using analysis of similarities (ANOSIM) in PRIMER (Clarke and Gorley 2006). The factors contributing to those differences were determined using SIMPER in PRIMER (Clarke and Gorley 2006).

As the data for Pielou's evenness in shrub mopane woodland met the assumptions for an analysis of variance (ANOVA) this, followed by Tukey's test to separate means at a significance level of 95%, was conducted in Genstat 12 (VSN-International 2009) to determine the effects of the three different forms of

utilization. Tukey's test was used to allow for uneven sample sizes in the data. The data for the independent variables, Hill's N_1, Hill's N_2 and total woody species density in shrub mopane woodland violated the assumptions of ANOVA. As this could not be rectified using transformations, the effects of the three different forms of utilization were determined using a non-parametric median test with pairwise comparisons to separate medians at a significance level of 95%. These analyses were conducted in SPSS (IBM 2010). The effects of the different forms of utilization on total woody species density and the diversity indices; Hill's N_1, Hill's N_2, Pielou's evenness and woody species richness in mixed thornveld were determined using an independent 2-sample t-test in SPSS (IBM 2010). In order to meet the t-test assumptions, the data for mixed thornveld woody species density were log transformed in Genstat 12 (VSN-International 2009).

5.3 RESULTS

5.3.1 Shrub mopane woodland

There were significant differences in sward cover under all three forms of utilization, while Sankuyo and Shorobe were significantly different from the wildlife management areas in terms of spizes composition and height class composition but not different to one another. Only Shorobe and the wildlife management area showed a significant difference in tree species composition (Table 5.1).

Table 5.1: ANOSIM analysis on the relative density of woody species composition, spizes composition and height class composition, and sward compositional cover between the three different forms of utilization in shrub mopane woodland. Significant values in bold

	p-value			
	Tree species	Spizes	Height class	Sward cover
SAN vs. SHO	0.785	0.263	0.06	**0.0003**
SAN vs. WMA	0.367	**0.001**	**0.001**	**0.001**
SHO vs. WMA	**0.011**	**0.001**	**0.006**	**0.014**

The main factors contributing to the significant difference between the tree species composition in the wildlife management area and in the grazing areas in Shorobe were the density of *Colophospermum mopane* and *Lonchocarpus nelsii*. Both of these species had a higher relative density in the wildlife management area. *C. mopane* accounted for 47.8% of the tree cover in the wildlife management area and only 38.5% in Shorobe, while *L. nelsii* contributed 24.6% to the woody cover in the wildlife management area and only 0.3% in Shorobe. These two species accounted for 25.2% and 17.0% of the dissimilarity between the shrub mopane woodland in the wildlife management area and Shorobe. Other species contributing between 5 and 10 % to the dissimilarity between the two regions were *Acacia erioloba*,

Acacia tortilis and *Gymnosporia senegalensis* all of which have a substantially greater density in Shorobe.

Table 5.2: Mean relative density of *Colophospermum mopane* spizes (%) and their contribution to the difference between the wildlife management area and Sankuyo and Shorobe in shrub mopane woodland from SIMPER analysis. Only those which contribute more than 5% to the dissimilarity are shown (* = this species did not contribute more than 5% to the dissimilarity between these forms of utilization). Height classes denoted using numbers 1 – 5 (1 = <0.49m, 2 = 0.5-0.99m, 3 = 1-1.99m, 4 = 2-2.99m and 5 = >3m) CMO = *Colophospermum mopane*

	Land Use			Contribution to dissimilarity (%)	
	SAN (goats)	SHO (cattle & goats)	WMA (wildlife)	SAN vs. WMA	SHO vs. WMA
CMO1	6.8	3.6	29.0	16.7	16.3
CMO2	12.5	*	4.0	7.5	*
CMO3	20.0	10.0	5.8	11.7	5.8
CMO4	10.4	8.7	7.7	7.0	5.5
CMO5	30.6	10.7	6.5	16.9	6.2

Table 5.3: Mean relative density of height classes (%) and their contribution to the difference between the wildlife management area and Sankuyo and Shorobe in shrub mopane woodland from SIMPER analysis

	Land Use			Contribution to dissimilarity (%)	
	SAN (goats)	SHO (cattle & goats)	WMA (wildlife)	SAN vs. WMA	SHO vs. WMA
<0.5m	12.1	18.7	43.0	30.1	33.9
0.5-1m	16.1	17.0	10.4	11.7	12.6
1-2m	21.5	30.4	16.2	16.8	74.1
2-3m	12.5	15.9	15.9	13.5	13.3
>3m	37.9	21.6	14.5	27.9	20.4

The main contributing factors to the significant difference in spizes composition between the wildlife management area and Sankuyo were the relative densities of *C. mopane* shorter than 0.5m and taller than 3m. These contributed to 16.7% and 16.9% of the dissimilarity between the two regions respectively. The density of *C. mopane* shorter than 0.5m was substantially greater in the wildlife management area, while the opposite was true for *C. mopane* taller than 3m (Table 5.2). A similar trend was observed in terms of height class across all species, with the wildlife management areas having a greater density of woody species shorter than 0.5m than Sankuyo and a lesser relative density of woody species taller than 3m (Table 5.3).

The density of *C. mopane* shorter than 0.5m was the major cause for the difference between the spizes composition of the wildlife management area and Shorobe although, unlike Sankuyo, the relative density of *C. mopane* taller than 3m did not show large differences (Table 5.2). This effect does not appear to be species specific, as a similar trend was observed in terms of height class across all species (Table 5.3).

Table 5.4: Mean grass cover (%) (with ecological status in brackets – I1 = Increaser 1, I2 = Increaser 2, I3 = Increaser 3) and the species contribution to the difference between the three different forms of utilization in shrub mopane woodland from SIMPER analysis. Only those which contribute more than 5% to the dissimilarity are shown (* = this species did not contribute more than 5% to the dissimilarity between these forms of utilization). Grass species abbreviations are explained in Appendix A

	Land Use			Contribution to dissimilarity (%)		
	SAN (goats)	SHO (cattle & goats)	WMA (wildlife)	SAN vs. SHO	SAN vs. WMA	SHO vs. WMA
AJU (I3)	3.8	*	2.6	*	5.7	*
Bare ground	46.9	77.8	71.3	39.1	33.3	36.6
ELE (I2)	*	0.1	4.1	*	*	6.9
HERB (I1)	34.7	10.0	11.3	29.8	31.7	20.0
SHI (I2)	5.0	1.0	0.8	5.8	6.0	*
UMO (I2)	7.3	3.4	4.1	10.5	10.3	10.8

The main reasons for the significant differences between the three types of utilization were firstly the amount of bare ground present, contributing to more than 30% of the dissimilarity, and the herbaceous plant cover, contributing to between 20 and 32% of the dissimilarity. Shorobe had the greatest amount of bare ground in the grazing areas, followed by the wildlife management area, while Sankuyo had substantially less. The reason for this may be that Sankuyo had more than 3 times the herbaceous cover present in either Shorobe or the wildlife management area. Sankuyo had five times the cover of *Stipagrostis hirtigluma* and double the cover of *Urochloa mossambicensis* than that which was recorded in either the wildlife management area or Shorobe. Sankuyo also had greater cover of *Aristida junciformis* than the wildlife management area, while the wildlife management area had slightly more *U. mossambicensis* and substantially more *Eragrostis lehmanniana* than Shorobe (Table 5.4).

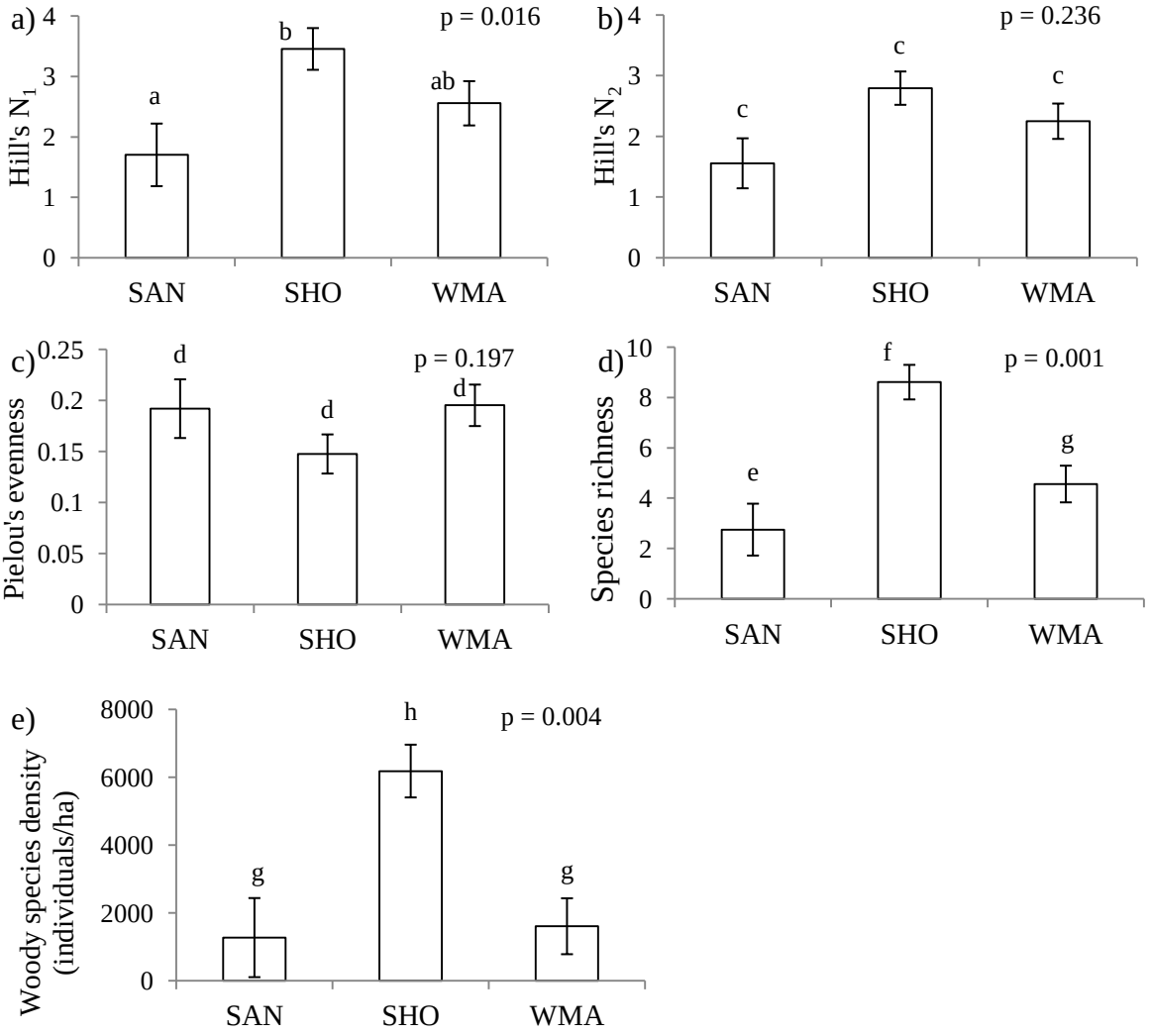

Figure 5.2: Mean values (±SE) for the diversity indices; Hill's N_1 (a), Hill's N_2 (b), Pielou's evenness (c) and Species richness (d), and woody species density (e) under three different forms of land use in shrub mopane woodland. Treatments with letters in common are not different.

Differences in utilization had a significant effect on Hill's N_1 ($p = 0.016$), species richness ($p = 0.001$) and woody species density ($p = 0.004$) but no effect on Pielou's evenness ($p = 0.197$) and Hill's N_2 ($p = 0.236$). Hill's N_1 was significantly higher in Shorobe than in Sankuyo; however neither was significantly different from the wildlife management area. This indicates that the areas utilized by cattle and goats in Shorobe had a greater diversity of abundant species than the areas utilized by goats only in Sankuyo, while there was no effect on the diversity of very abundant species. Shorobe also had a significantly greater woody species density and woody species richness than both Sankuyo and the wildlife management area (Figure 5.2).

5.3.2 Mixed thornveld

Grazing by cattle and goats in mixed thornveld had a significant effect on tree species relative density ($p = 0.001$), spizes relative density ($p = 0.002$), height class relative density ($p = 0.026$) and sward cover ($p = 0.008$).

The wildlife management area was dominated by *A. erioloba* (68.9%), while Shorobe had less than a quarter of that cover (16.0%) and was rather dominated by *A. tortilis* (31.8%). *A. tortilis* accounted for only 8.9% of the woody density in the wildlife management area. The differences between these two species contribute 35.7% and 21.1% to the dissimilarity between the wildlife management area and Shorobe respectively. In addition *Combretum imberbe, Hypheane petersiana* and *Ziziphus mucronata*, all of which are more abundant in Shorobe, contribute between 6 and 10% to the dissimilarity between the two areas.

The main factors affecting the difference in spizes composition between Shorobe and the wildlife management area were *A. erioloba* taller than 3m and shorter than 0.5m. The tree cover in the wildlife management area consisted of 33.3% *A. erioloba* taller than 3m, compared to only 10.6% in Shorobe. When looking at *A. erioloba* shorter than 0.5m the difference was even greater, with the wildlife management area having a relative density of 18.0% and Shorobe only 0.3%. These differences contributed 17.1% and 10.1% to the dissimilarity between Shorobe and the wildlife management area respectively. *Acacia tortilis* and *H. Petersiana* between one and two metres tall also contributed more than 5% to the dissimilarity, with Shorobe having substantially greater proportions of these two species.

Overall the woody cover in the wildlife management area is dominated by trees taller than 3m (36.5%) and shorter than 0.5m (30.5%), while the woody cover in Shorobe is dominated by trees between 1 and 2 metres in height (35.9%).

Shorobe has significantly more bare ground (53.7%) than the wildlife management area (43.9%), contributing 18.5% to the dissimilarity between the two areas. The most dominant grass in the wildlife management area is *Digitaria eriantha* (16.2%), however this species is barely present in Shorobe (0.5%). This difference contributed 16.8% to the dissimilarity between Shorobe and the wildlife management area. *Eragrostis lehmanniana* is four times more abundant in the wildlife management area, while *Cynodon dactylon, U. mossambicensis* and *Chloris virgata* are all more abundant in Shorobe. These differences contribute between 6 and 10% to the dissimilarity between the two areas.

Table 5.5: Data means (±SE) and p-values of an independent two-sample t-test between the wildlife management area (WMA) and Shorobe (SHO) for Hill's N_1, Hill's N_2, Pielou's evenness, species richness and woody species density in mixed thornveld. Significant p-values in bold

	Hill's N1	Hill's N2	Pielou's evenness	Species richness	Woody species density (individuals/ha)
WMA	1.88 ± 0.196	1.23 ± 0.307	0.15 ± 0.030	2.88 ± 0.427	213.54 ± 47.464
SHO	3.20 ± 0.464	2.98 ± 0.399	0.23 ± 0.249	5.00 ± 0.985	916.66 ± 236.894
p-value	**0.008**	**0.041**	**0.040**	0.054	< **0.001**

Grazing by cattle, goats and donkeys in mixed thornveld had a significant effect on Hill's N_1, Hill's N_2, Pielou's evenness and total woody species density with all of these factors having greater values in Shorobe than in the wildlife management area. Species richness was the only factor calculated that was not affected (Table 5.5).

5.4 DISCUSSION

5.4.1 Shrub mopane woodland

Woody layer species composition in shrub mopane woodland was only affected by cattle utilization, while both utilization by goats alone and the combination of cattle and goats affected woody layer height structure and the height structure of specific species or spizes.

In the wildlife management area shrub mopane woodland was dominated by *Colophospermum mopane* and *Lonchocarpus nelsii*, however outside the veterinary cordon fence shrub mopane woodland was dominated by *Acacia erioloba, Acacia tortilis* and *Gymnosporia senegalensis*. Although *C. mopane* has a fairly high crude protein content, approximately 12% (Roodt 1998a) livestock will avoid browsing it if alternatives are available as the mature leaves are highly aromatic (Aubrey 2004). The young leaves and slow-growing seedlings are more palatable and will be readily browsed (Aubrey 2004) along with the dry leaves and pods which retain much of their crude protein level after falling to the ground, making it a valuable source of winter forage (Roodt 1998a). It is therefore expected that the major differences in *C. mopane* relative density are observed in the seedling layer. This effect can be seen not only in the areas utilized by cattle and goats but also those browsed by goats alone, although it is not as marked in these areas. This effect is apparent to differing degrees across woody species in the livestock utilization areas and has also been observed in Ethiopia where heavily browsed areas show a distinct lack of recruitment (Yayneshet et al. 2009), particularly as a result of seedling predation by medium size herbivores (Moe et

al. 2009). This effect is however dependant on browser stocking rate as moderate utilization has been found to stimulate shoot production (Oba 1998). Like *C. mopane*, *L. nelsii* is slow-growing, but its leaves are non-aromatic and thus more palatable to browsers despite the mature leaves becoming large and leathery (Roodt 1998a, Coates Palgrave 2003). However it is more sensitive to disturbance than *C. mopane* (Roodt 1998a) and is thus more severely affected by livestock utilization, resulting in a relative density of less than 1% in the communal grazing areas utilized by cattle and goats south of the veterinary cordon fence.

Surprisingly the leguminous species, *A. erioloba* and *A. tortilis* have a greater abundance in the areas utilized by cattle and goats than in the areas utilized by wildlife despite having a higher leaf and pod crude protein content than the heavily browsed *C. mopane* and being one of the first woody species to have green foliage in late winter (Roodt 1998a). The same trend is seen in the highly palatable *G. senegalensis*. It would be expected that the seedlings of these palatable species would be utilized to the same extent as those of *C. mopane* and *L. nelsii*, however these *A. erioloba*, *A. tortilis* and *G. senegalensis* all bear large thorns (Roodt 1998a) which discourage livestock from consuming the entire seedling or branch (Cooper and Owen-Smith 1986, Gowda 1996), which is possible with the non-thorny *C. mopane* and *L. nelsii*. The large straight thorns on *A. erioloba* and *G. senegalensis* are an effective deterrent to large browsers as they are unable to select the leaves between the thorns, as small and medium size browsers can. While smaller hooked thorns, such as those occurring in combination with straight thorns on *A. tortilis*, are a more effective deterrent against the smaller, more selective browsers (Cooper and Owen-Smith 1986).

Utilization by goats alone significantly decreased the diversity of abundant species, represented by Hill's N1, as well as the overall species richness of the woody layer, while utilization by both cattle and goats produced the opposite effect, increasing Hill's N1 diversity and species richness. This is somewhat different to observations by Metzger *et al*. (2005) in the semi-arid regions of Kenya, who noted that heavy utilization had no effect on species diversity, while Haarmeyer *et al*. (2010) and Wasiolka and Blaum (2011) noted a decrease in species richness, similar to that seen in the areas utilized by goats alone, after utilization by livestock in the succulent karroo region of South Africa and the southern Kalahari, South Africa respectively.

The abundance of herbaceous annuals in the Sankuyo livestock area utilized by goats alone is an indication of undergrazing (Camp and Hardy 1999). However the presence of the increaser 2 species, *Stipagrostis hirtigluma* and *Urochloa mossambicensis* and the increaser 3 species, *Aristida junciformis*

suggests overutilization (van Oudtshoorn 1999). As the increaser 2 and increaser 3 species are climax and sub-climax species and are more abundant in Sankuyo than in the wildlife management area, it is likely that their presence is as a result of past overgrazing, dating back to when the Sankuyo community kept cattle. The extensive bare ground and low cover of herbaceous annuals present outside the veterinary cordon fence, coupled with the presence of increaser 2 species, *Eragrostis lehmanniana*, *Urochloa mossambicensis* and *Stipagrostis hirtigluma* may indicates that the area is being overutilized. *Eragrostis lehmanniana* and *U. mossambicensis* occur in slightly greater abundances in the wildlife management area than in Shorobe, however this does not indicate that the wildlife management area is more intensely utilized, but rather that these two fairly palatable species are being utilized in Shorobe as little else is available. As one of the first species to start growing in spring (van Oudtshoorn 1999), *E. lehmanniana* is prone to selective overutilization, while *U. mossambicensis* is tolerant of fairly dense shading (Roodt 1998a) and is thus one of the few species available in the dense shrub mopane woodland regions of Shorobe. By contrast *S. hirtigluma* is only readily grazed in the early growth stages (Chippindall and Crook 1976) and is therefore not as intensely utilized. This overutilization of the grass sward is intensified as there is little woody browse available to cattle in the shrub mopane woodland regions. Although cattle are predominantly grazers they may include as much as 50% browse in their diet depending on the season and availability of grazing (Moleele 1998, Owen-Smith 1999). In Botswana cattle have been found to favour the non-thorny *Grewia* species, *Boscia albitrunca* and *Terminalia sericea* and to some extent the thorny *Dichrostachys cinerea* (Moleele 1998) although these thorny species with small leaves interspersed among the thorns are difficult for cattle to utilize owing to their non-selective wrap, pull and tear method of ingesting food (Owen-Smith 1999). The majority of the non-thorny woody cover in Shorobe is the aromatic *C. mopane* which livestock will browse if they are accustomed to it but tend to avoid if possible (Aubrey 2004).

There is evidence of some degree of bush thickening in the shrub mopane woodland regions of Shorobe as the total woody species density is more than three times that observed in Sankuyo or the wildlife management area. This bush thickening may be attributed to the pressure exerted on the grass sward by the cattle population and shading from the existing woody layer resulting in a lack of grass competition for resources (Scholes and Archer 1997), insufficient grass fuel load to support hot fires which decrease the woody density (Trollope 1974) and an increase in available resources allowing woody plants to grow unhindered. This thickening is most evident in the 1 – 2m size class indicating that some historical event allowed for a mass germination of woody species. Providing the goat population in Shorobe remains of a similar size it is unlikely that this bush thickening will worsen as woody plants in the shrub mopane woodland are unlikely to survive past the seedling stage without being totally consumed.

5.4.2 Mixed thornveld

As was observed in shrub mopane woodland, utilization by a combination of cattle and goats significantly affected all the factors examined when compared to similar areas utilized by wildlife alone.

Cattle and goat utilization had the opposite effect on *Acacia erioloba* density in mixed thornveld, than was observed in shrub mopane woodland, with *A. erioloba* density being substantially greater in the wildlife management area. This difference in density was particularly evident in *A. erioloba* taller than 3m and shorter than 0.5m, with both height classes being abundant in the wildlife management area and fairly scarce in Shorobe, south of the veterinary fence. As *A. erioloba* makes good firewood (Roodt 1998a) this may account for the low density of large *A. erioloba* in Shorobe, however it is more likely for people to collect fallen branches for firewood, rather than cut down an entire tree. It is likley the lack of large *A. erioloba* in Shorobe is the Tsetse fly eradication attempts conducted in the 1960s. The shady foliage of these large *A. erioloba* was considered perfect habitat for the fly and as a result many large trees were felled (Roodt 1998a). Browsing by goats is likely to be the reason behind the lack of *A. erioloba* seedlings in Shorobe. In the absence of non-thorny seedlings, browsers will readily browse the palatable leguminous species, consuming small seedlings whole, or browsing larger seedlings so heavily they are unable to survive (Moe et al. 2009, Yayneshet et al. 2009). Similar observations were made in communal areas in Namibia where browsing by goats removed large numbers of newly emerged *A. erioloba* seedlings (Moser-Norgaard and Denich 2010).

The overall structural composition in the wildlife management area is vastly different to that observed in Shorobe. In the wildlife management area the woody vegetation structure has a bimodal distribution with more than 30% of the woody cover taller than 3m and approximately 30% shorter than 0.5m, while the woody cover in Shorobe had a unimodal distribution with the bulk of the vegetation falling into the 1 – 2m height class. Much of the woody cover falling into this height class is comprised of *Acacia tortilis* and *Hyphaene petersiana* both of which are more dominant in Shorobe than in the wildlife management area. Although the woody species density in mixed thornveld is much less than that in shrub mopane woodland, it is still apparent that some form of bush thickening is taking place, with Shorobe having a woody species density four times greater than that observed in similar regions within the wildlife management area. Much of this bush thickening is as a result of even aged stands of the recognised encroacher *A. tortilis* (Timberlake 1980, Moleele et al. 2002), a species which often occurs in regions which have been modified by livestock utilization (Dangerfield et al. 1996). Despite being a palatable legume, utilization by livestock has not been found to decrease the overall height of the plants in other

studies, however the number of shoots produced and shoot length decreased indicating some form of impact (Dangerfield et al. 1996). *Hyphaene petersiana* is a highly utilized species in the Okavango Delta with the leaves being used for basket weaving, the seeds being used to make ornaments and buttons and the sap used to make palm wine (Forrester et al. 1989, Roodt 1998a, Harrison 2006). One of the more popular uses in the Shorobe area is producing palm wine. In order to do this the area around the plant is burnt then any remaining leaves are cut off and the growing tip is cut to form a point. Incisions are then made near the tip and cut sections of leaf blade are inserted into them, channelling the sap into the waiting receptacle. Although the same stump may be used the following season the plant rarely survives longer than that. Although these plants die, the burning involved in preparing the plant accelerates germination of any mature *H. petersiana* seeds present (Roodt 1998a) thereby assisting in the repopulation of the area and accounting for the large number of short *H. petersiana* observed. The commercial production of baskets woven from the young leaves of *H. petersiana* is also likely to contribute to this trend towards a shorter population structure as continual leaf harvesting results in the production of vegetative suckers creating a predominantly shrubby, multi-stemmed *H. petersiana* population (Cunningham and Milton 1987, Sullivan et al. 1995).

Combretum imberbe and *Ziziphus mucronata* were also observed in greater density in Shorobe than in the wildlife management area. *Combretum imberbe* is heavily utilized by elephant (Ben-Shahar 1993) and although wildlife moves outside the veterinary cordon fence the number of individuals is minimal in comparison to those existing inside the veterinary cordon fence. Evidence of elephant in Shorobe has been seen on numerous occasions; however this is more likely to be as a result of solitary individuals moving through the area than resident groups, thus having little effect on the density of *C. imberbe*. Similarly *Z. mucronata* is more heavily utilized within the wildlife management area as it has a high nutritional value but is not particularly palatable (Roodt 1998a) and will not be browsed by livestock in its mature state if more palatable alternatives are available (Venter and Venter 2002).

Contrary to the observations of Metzger et al. (2005) and Anderson and Hoffman (2007) the diversity of abundant (Hill's N1) and very abundant (Hill's N2) species increased with utilization by cattle and goats. Unlike shrub mopane woodland and contrary to the observations by Wasiolka and Blaum (2011) where the species richness decreased with livestock utilization, species richness remained unchanged. Similar observations were made by Haarmeyer (2010). Also contrary to the observations in shrub mopane woodland, Pielou's evenness co-efficient was greater in the wildlife management area, indicating that it was dominated by a specific species or suite of species. This is further evidenced by the 69% cover of *A. erioloba* in the wildlife management area.

As observed in shrub mopane woodland, livestock utilization in mixed thornveld resulted in large areas of bare ground and a dominance of pioneer increaser 2 species in the remaining sward indicating severe overgrazing (Camp and Hardy 1999), while the sward in the wildlife management area is dominated by the decreaser *Digitaria eriantha* (van Oudtshoorn 1999). Despite being an increaser 2 species (van Oudtshoorn 1999) *E. lehmanniana* is four times more abundant in the wildlife management area than in Shorobe. This can be attributed to the fact that it is one of the first species to start growing in spring (van Oudtshoorn 1999) and thus, as seen in shrub mopane woodland, would be overgrazed in the communal grazing areas but not in the wildlife management area as most wild grazers move onto the key resources areas, such as floodplains and perennial swamps in the north, for the winter. Of the increaser 2 species present in Shorobe, *Chloris virgata* and *U. mossambicensis* are both known to increase as a result of livestock grazing (Haarmeyer et al. 2010) and *Cynodon dactylon* is a creeping perennial common in heavily grazed areas (Yayneshet et al. 2009).

5.5 CONCLUSION

There is evidence of overutilization of the grass sward and bush encroachment in both shrub mopane woodland and mixed thornveld in the regions utilized by both goats and cattle, while substantial cover of herbaceous annuals in the shrub mopane woodland areas utilized by goats alone indicates underutilization. In order to improve the sward condition in the areas utilized by cattle and goats some form of livestock management involving resting of the grazing areas and burning in order to reduce the abundance of increaser 2 species needs to be implemented, however this presents a challenge in communal areas as a lack of ownership of the land often prohibits effective grazing management.

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CHAPTER 6: ENVIRONMENTAL CONDITIONS INFLUENCING THE OCCURRENCE OF *PECHEUL-LOESCHEA LEUBNITZIAE*

6.1 INTRODUCTION

Pecheul-Loeschea leubnitziae is a woody shrub belonging to the family Asteraceae and the tribe Inuleae (Roodt 1998, IZIKO 2011). Asteraceae is one of the largest flowering plant families with over 25 000 species globally (Kew 2011) and 2 300 species in southern Africa (Herman 2004). Inuleae in turn is the largest tribe in Asteraceae comprising 152 genera (Pullaiah 1979). Plant growth habit in this family is highly variable with species ranging from small herbs to shrubs and trees (Herman 2004). The flowering parts of this family are a collection of florets arranged in an inflorescence (Kew 2011). These inflorescences usually comprise of a large number of small disc florets surrounded by an outer ring of ray florets with a large ligulate corolla (Small 1916). The seeds produced by species in this family often have a feathery pappas which aids in wind distribution (Herman 2004, Kew 2011).

This efficient method of seed distribution has resulted in many of the plants in this family being regarded as weeds (Herman 2004, Kew 2011).One such weed is *Pecheul-Loeschea leubnitziae* (Wells et al. 1986). It is a perennial shrub, with woody stems and semi-deciduous leaves (Wells et al. 1986). The plant is strongly aromatic and the grey leaves are covered in glandular hairs (Hyde et al. 2011). Although cattle, goats and donkeys will readily browse it, this is usually done when there is little else available (Roodt 1998, Strobach 2000). For this reason it is considered unpalatable and undesirable for stock owners to have in their grazing lands. This pioneer species occurs in the dry terrestrial zones of the summer rainfall regions (Wells et al. 1986) and invades trampled areas with low basal cover (Strobach 2001). It is considered to be an indicator of both dry floodplains and overgrazing (Burke 2000, Huntsman-Mapila et al. 2003, Murray-Hudson 2009). Cover of *P. leubnitziae* has been observed to increase with increasing veld degradation and extensive cover occurs in heavily degraded veld (Strobach 2000).

The majority of predictive models for the Okavango Delta predict a decrease in groundwater and a general drying with progressing climate change. This will result in a decrease in the extent of swamp and floodplain communities and an increase in dry grassland and woodland communities (Burg 2007). As large portions of the dry grassland and woodland communities in the south eastern Okavango Delta already have extensive stands of *P. leubnitziae* it is expected that climate change induced drying will result in an increase in the extent of the species. As *P. leubnitziae* tends to form fairly dense monotypic stands of approximately 1.5m in height, which leads to the development of a grass sward dominated by shade-tolerant species with low grazing values and a decrease in visibility for photographic safaris. This

expected increase raises concerns, particularly in terms of the negative effect it may have on both the carrying capacity of the dry grassland and woodland communities and wildlife tourism in the area. As little is known about the population dynamics of *P. leubnitziae* other than its tendency to colonise dry, degraded areas (Burke 2000, Strobach 2001) it is currently impossible to develop any form of management plan to limit the spread of the species and minimise its negative effects on land use potential and the tourism industry.

The objective of this study was to determine the effects of land use, fire, vegetation characteristics, woody species density and soil characteristics affecting the occurrence of *P. leubnitziae*.

6.2 METHODS

6.2.1 Experimental design

The experimental design comprised of one hundred and two spatially independent sites located within three areas under different management practices (Davies et al. 2006, Holmes 2007, Cleary et al. 2010). In order to determine the effects of different forms of utilization eight of the sites were located in the livestock grazing areas surrounding Sankuyo, thirty in Shorobe and sixty-four in the wildlife management area (WMA).

Sankuyo (SAN) is located within the WMA, so grazing is restricted to the areas within and immediately adjacent to the village in order to minimise the loss of livestock to predators (Figure 6.1). Consequently the number of sample sites in Sankuyo was limited to eight and these were located fairly close to one another. Sankuyo and the adjacent grazing areas are located in the vegetation management unit shrub mopane woodland. As cattle are not permitted within the WMA the grazing livestock in Sankuyo is limited to donkeys and goats.

Shorobe (SHO) is located outside of the veterinary cordon fence. Therefore, it does not have the predator related restrictions on grazing areas experienced by livestock owners in Sankuyo (Figure 6.1). Shorobe has a population approximately four times larger than Sankuyo and thus would be expected to have a greater number of livestock. It does however cover an area approximately twenty times larger than Sankuyo. The grazing areas in Shorobe fall under shrub mopane woodland to the east and mixed thornveld to the west of the town centre and main road, and the livestock present consist of cattle, goats and donkeys. Of the thirty sites sampled in Shorobe, eighteen were located in shrub mopane woodland and twelve in mixed thornveld.

Within the WMA sixteen sites were sampled in each of the four vegetation management units; tall mopane woodland, shrub mopane woodland, mixed broadleaf woodland and mixed thornveld. These sites were widely scattered across NG33, NG34 and Moremi Game Reserve (Figure 6.1). These areas are adjacent to one another and thus receive similar rainfall and have similar underlying soil types. These areas are all exclusively utilized by wildlife and there are no fences separating these areas so there a few differences in terms of grazing pressure.

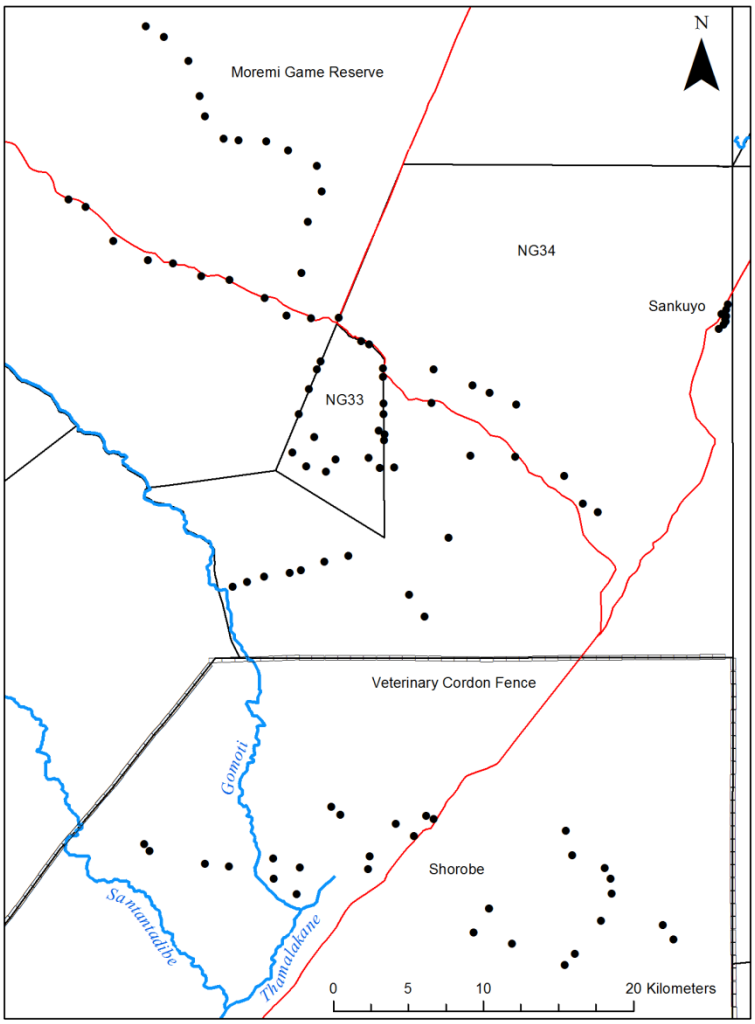

Figure 6.1: Geographic locations of sample sites in Shorobe, Sankuyo and the Wildlife Management Area. Roads are indicated in red and rivers in blue.

6.2.2 Data Collection

6.2.2.1 Vegetation

Each sample site covered an area of approximately 100m by 50m. At each site three transects (100m by 3m) were set out approximately 5m apart in order to ensure independence. GPS co-ordinates were

recorded at the start and end points of each transect to allow for repeat sampling. The species of each woody plant rooted within the transect area was then recorded.

6.2.2.2 Soil

At each site, three randomly located topsoil (the top 15cm) and subsoil (below 40 cm) sub-samples were taken and combined forming one topsoil and one subsoil sample for each site. Owing to the sandy nature of the soils in the study area these samples were then analysed for particle size composition, sand fraction composition and pH. Soil particles were classed into the following categories, clay (<0.002mm), silt (0.05 – 0.002mm) and sand (2.0 – 0.05mm). In addition infiltration rate was measured using a mini disc infiltrometer manufactured by Decagon Devices, USA. This was done at three randomly selected locations within the sample site to determine a mean infiltration rate for each site.

6.2.2.3 Burning History

The sites were classified as burnt or unburnt according to the fire history of the previous six years. This was done by mapping fire distribution and frequency from 2003 – 2009 in ArcMap 10 (ESRI 2010) using active fire data downloaded from the University of Maryland's Fire Information for Resource Management System website (NASA/University-of-Maryland 2002, Davies et al. 2009). All burnt sites were located in regions which had burnt in a single fire event two years prior to sampling.

6.2.2.4 Extent of *Pecheul-Loeschea leubnitziae* cover

In addition the aerial cover of *P. leubnitziae* at each site was visually estimated to the nearest 10%. *Pecheul-Loeschea leubnitziae* aerial cover and GPS co-ordinates were also recorded at an additional two hundred and fifty-six sites distributed throughout NG33, NG34 and Moremi Game Reserve. Environmental variables were not recorded at these sites.

6.2.3 Data Analysis

6.2.3.1 Preliminary Analyses

The transect data were used to calculate the density (individuals per hectare) of each tree species and total woody density. As *P. leubnitziae* is a deep-rooted species it was important to determine if the topsoil and subsoil characteristics were influencing *P. leubnitziae* occurrence independently. This was done using a Mantel test in PC-ORD (McCune and Mefford 1997). Redundant variables were then identified and removed using correlation analysis in GenStat 12 (VSN-International 2009). The variables identified as closely correlated were removed from further analyses.

6.2.3.2 Data Exploration

To describe the overall effects of the environmental variables on the cover of *P. leubnitziae* the following preliminary analyses were conducted. For the three qualitative environmental variables; vegetation management unit (VMU), utilization and fire history, the frequency and proportion of sites with *P. leubnitziae* present within each category, as well as the maximum cover and average cover was calculated, while for the three quantitative environmental variables; soil pH, soil sand content and total woody species density, *P. leubnitziae* cover was plotted against each variable using scatter plots.

6.2.3.3 Model Development

As the overall frequency occurrence for the aerial cover of *P. leubnitziae* was strongly positively skewed the data were converted to presence-absence. The binomial distribution of this response variable allowed it to be modelled using a generalized linear model (GLM) with a logit link function. This was done in GenStat 14 (VSN-International 2011) using an all subsets regression with all possible regression models. The best model was determined using Akaike's information criterion (AIC) (Anderson et al. 1994). AIC is calculated using the following equation: AIC = residual deviance + 2 * K, with K being the number of parameters used in the model. This balances the fit of the model against the number of parameters used. The model with the smallest AIC and a difference of at least 2 AIC units from other models was accepted as the most accurate model. When models had an AIC value differing by less than 2 AIC units, the models using the least variables was chosen (Anderson et al. 1994).

When the all subsets regression using generalised linear modelling (GLM) showed the main effects of variables to be significant, the interactions of these variables were added to the model. The significance of these interactions was determined by examining the significance given by the accumulated analysis of deviance after running a GLM with a logit link function in Genstat 14 (VSN-International 2011). As all four VMUs and a matrix of burnt and unburnt areas were not available under all three forms of land utilization, the effects of type of land utilization were investigated, by removing the fire regime and VMU parameters from the dataset, and running an all subsets regression using a GLM.

6.2.3.4 Extent of *Pecheul-Loeschea leubnitziae* cover

The *Pecheul-Loeschea leubnitziae* aerial cover data collected at the one hundred and two transect sites and the additional two hundred and fifty-six sites aerial cover sampling sites were mapped in ArcGIS 10 (ESRI 2010) using proportional symbols to highlight regions of extensive *P. leubnitziae* cover.

6.3 RESULTS

6.3.1 Preliminary analyses

A Mantel test found the topsoil and subsoil qualities to be closely correlated (r = 0.73, p = 0.001) indicating that these two soil layers were not influencing *P. leubnitziae* occurrence independently. As a result analyses were performed on the topsoil data only. Correlation analysis showed a high positive correlation between topsoil silt and clay content and between topsoil sand content and infiltration. In addition topsoil silt and clay content were negatively correlated with topsoil sand content and infiltration rate (Table 6.1). For this reason topsoil sand content and topsoil pH were the only two soil variables included in the modelling process.

Table 6.1: Correlations between the soil properties of the topsoil layer across the four vegetation management units; tall mopane woodland, shrub mopane woodland, mixed broadleaf woodland and mixed thornveld

Clay					
Infiltration	-0.616				
Sand	-0.916	0.717			
Silt	0.681	-0.698	-0.918		
pH	0.444	-0.385	-0.460	0.392	
	Clay	Infiltration	Sand	Silt	pH

6.3.2 Data exploration

Pecheul-Loeschea leubnitziae was present in a substantially greater proportion of the mixed broadleaf woodland and mixed thornveld sites than the tall mopane woodland and mixed mopane woodland sites (Table 6.2). The average cover of *P. leubnitziae* in mixed broadleaf woodland and mixed thornveld was fairly similar, while the maximum cover was vastly different. The maximum *P. leubnitziae* cover encountered in mixed broadleaf woodland was 50%, while in mixed thornveld it was 90% (Table 6.2). In terms of utilization, the wildlife management area has *P. leubnitziae* present in 54% of the sites sampled, while it was present in Shorobe and Sankuyo in 37% and 25% of the sites sampled respectively. The average *P. leubnitziae* cover in the wildlife management area was slightly lower than the average cover in Shorobe however the maximum cover encountered in the wildlife management area was 90%, while in Shorobe it was only 50%. Sankuyo had substantially lower *P. leubnitziae* cover than both the wildlife management area and Shorobe (Table 6.2). There was little difference in the *P. leubnitziae* cover between the burnt and unburnt areas with *P. leubnitziae* being encountered in approximately half the sites sampled. The maximum cover encountered in the unburnt areas was somewhat greater than that observed in the burnt areas (Table 6.2).

Table 6.2: Frequency and proportion of sites in each category of the variables, vegetation management unit (VMU), location and fire history with *Pecheul-Loeschea leubnitziae* present and the maximum *P. leubnitziae* cover and mean *P. leubnitziae* cover in each of these categories

		Frequency	Proportion of sites (%)	Maximum cover (%)	Average cover (%)
VMU	Tall mopane woodland (PM)	2	12	5	5
	Short mopane woodland (MM)	9	21	40	9
	Mixed broadleaf woodland (BL)	12	75	50	17
	Mixed thornveld (TH)	25	89	90	16
Utilization	Sankuyo (SAN)	2	25	5	5
	Shorobe (SHO)	11	37	60	16
	WMA	35	54	90	12
Fire history	Burnt (B)	18	56	50	10
	Unburnt (UNB)	30	42	90	15

When plotted against pH and soil sand content the *P. leubnitziae* cover data were negatively skewed, with greater cover of *P. leubnitziae* occurring at pH levels greater than 4 and soils comprised of more than 60% sand (Figure 6.2). The opposite was apparent when plotted against total woody density, where the *P. leubnitziae* cover data were positively skewed (Figure 6.2).

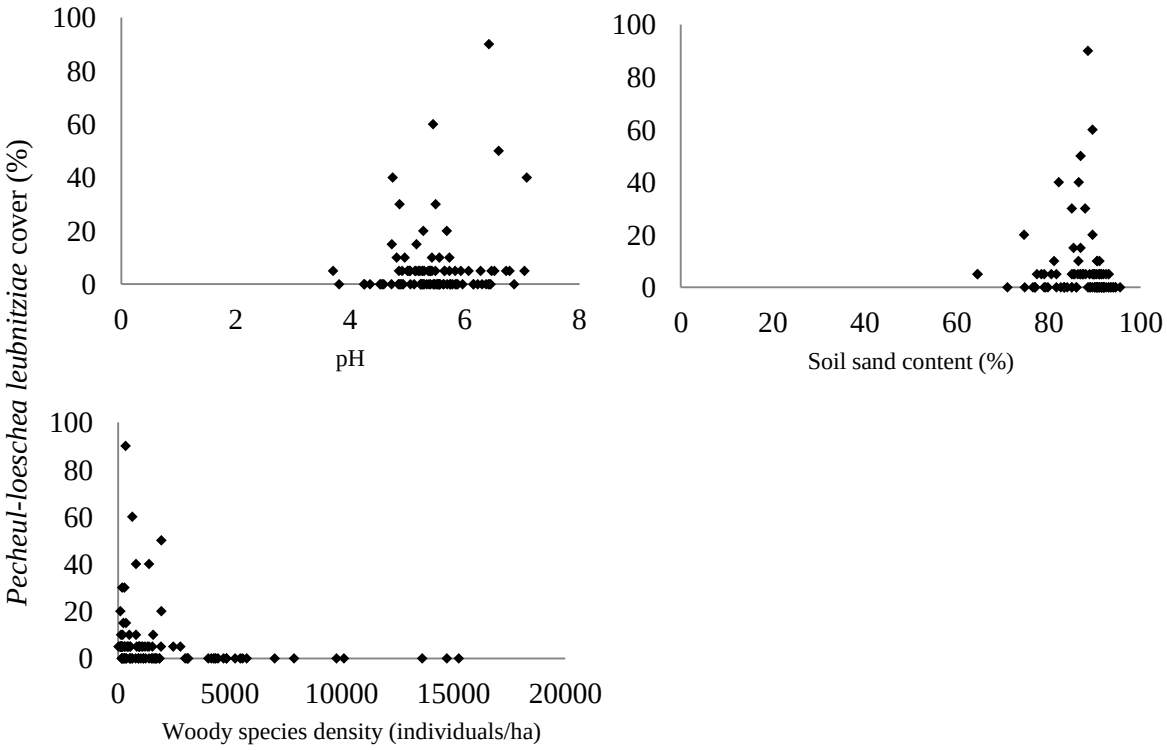

Figure 6.2: *Pecheul-Loeschea leubnitziae* cover (%) according to soil pH, soil sand content (%) and woody species density (individuals per ha).

6.3.3 Model development

Generalized linear modelling of individual parameters, using a logit link function, found total woody density and VMU to have a significant effect on the occurrence of *P. leubnitziae*. The fire regime under discussion, type of land use, soil pH and soil sand content had no significant effect on the occurrence of *P. leubnitziae* (Table 6.3).

Akaike's Information Criterion produced by all subsets regression conducted using only the two parameters found to have a significant effect on the occurrence *P. leubnitziae* presence revealed the best model to be that which included both total woody density and VMU. The AIC for this model was 107.49. The model including all the significant parameters had an AIC of 109.00 which is less than 2 AIC units greater than the two parameter model, the requirement for any one model to be significantly better than another (Anderson et al. 1994), however the model with a lower number of parameters was accepted as the best fit (Table 6.4). GLM found the interaction between these two parameters to have a significant

effect on the likelihood of occurrence of *P. leubnitziae* presence and this interaction was therefore included in the final model (Table 6.5).

Table 6.3: Summary of single parameter fitted incidence models for *Pecheul-Loeschea leubnitziae* using generalized linear modelling

	df	Significance	Deviance	AIC
Burn	1	0.267	140.58	161.31
Total woody density	1	**<0.001**	108.24	125.12
Utilization	2	0.227	138.15	161.59
VMU	3	**<0.001**	93.02	112.09
Soil sand content	1	0.274	140.63	161.37
pH	1	0.479	141.60	162.46

Table 6.4: Summary of all subsets fitted incidence models for *Pecheul-Loeschea leubnitziae* using generalized linear modelling

	1	2	3
Total woody density	-	**<0.001**	**0.015**
VMU	**<0.001**	-	**<0.001**
Deviance	90.75	108.07	85.34
AIC	113.14	128.83	109.00

Table 6.5: Accumulated analysis of deviance for final fitted incidence model for *Pecheul-Loeschea leubnitziae* using generalized linear modelling

	df	Deviance	Significance
+VMU	3	49.2898	<0.001
+Density	1	34.072	<0.001
+Density.VMU	7	57.5613	<0.001
Residual	91	1.3891	
Total	102	142.3122	

The interaction between VMU and density accounted for most of the variance in the model, followed by VMU and density (Table 6.5). Total woody density was found to have a negative effect on *P. leubnitziae* cover, with decreasing likelihood of *P. leubnitziae* occurrence with increasing total woody density (Table 6.6). *Pecheul-Loeschea leubnitziae* was five times more likely to occur in mixed thornveld than in mixed broadleaf woodland, while it is five times less likely to occur on shrub mopane woodland. *Pecheul-Loeschea leubnitziae* was least likely to occur in tall mopane woodland (Table 6.6).

Table 6.6: Estimates of the final model parameters for the fitted incidence model for *Pecheul-Loeschea leubnitziae* using generalized linear modelling. Mixed broadleaf woodland was used as a baseline for comparison for qualitative parameters

	Estimate	s.e.	t(*)	t pr.	Likelihood of occurrence
Constant	1.1950	0.9100	1.31	0.190	3.302
VMU MM	-1.5300	1.0800	-1.42	0.156	0.217
VMU PM	-2.4500	1.5200	-1.61	0.107	0.086
VMU TH	1.7300	1.2800	1.35	0.179	5.630
Density	-0.0001	0.0010	-0.14	0.890	0.999
Density.VMU MM	-0.0003	0.0010	-0.28	0.776	1.000
Density.VMU PM	-0.0002	0.0011	-0.20	0.845	1.000
Density.VMU TH	-0.0010	0.0012	-0.81	0.418	0.999

The interaction between VMU and total woody density showed an inverse relationship with likelihood of *P. leubnitziae* occurrence decreasing with increasing total woody density in all four VMUs (Table 6.5, Figure 6.2). The likelihood of occurrence of *P. leubnitziae* in mixed thornveld, shrub mopane woodland and tall mopane woodland was compared against the likelihood of occurrence in mixed broadleaf woodland (Figure 6.2). Although the likelihood of occurrence in mixed thornveld is extremely high at low total woody density this VMU showed the steepest decline as total woody species density increased (Figure 6.2). Tall mopane woodland and shrub mopane woodland showed a 20% and 40% likelihood of occurrence of *P. leubnitziae* at low total woody species density respectively. This likelihood decreased to less than 10% at total woody species density of 6000 individuals per hectare (Figure 6.2).

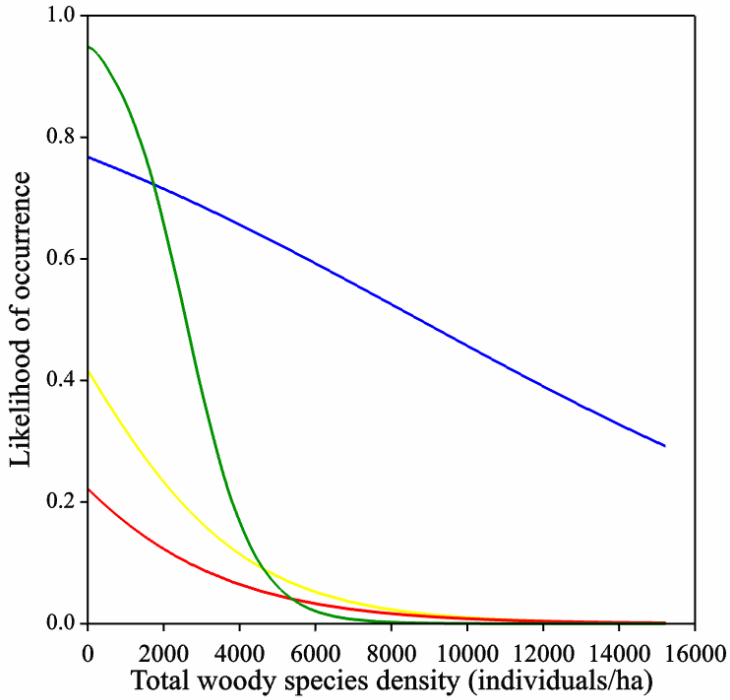

Figure 6.3: Effect of total woody species density on the likelihood of presence of *Pecheul-Loeschea leubnitziae* in each of the four management units; tall mopane woodland (red), shrub mopane woodland (yellow), mixed thornveld (green) and mixed broadleaf woodland (blue).

6.3.3.1 Extent of *Pecheul-Loeschea leubnitziae* cover

Pecheul-Loeschea leubnitziae aerial cover is highest in the western regions of NG33 and NG34 and directly adjacent to the Gomoti River in southern Moremi Game Reserve. *Pecheul-Loeschea leubnitziae* presence in Shorobe is limited to those sites on the western side of the village adjacent to the Gomoti and Santantadibe Rivers (Figure 6.4).

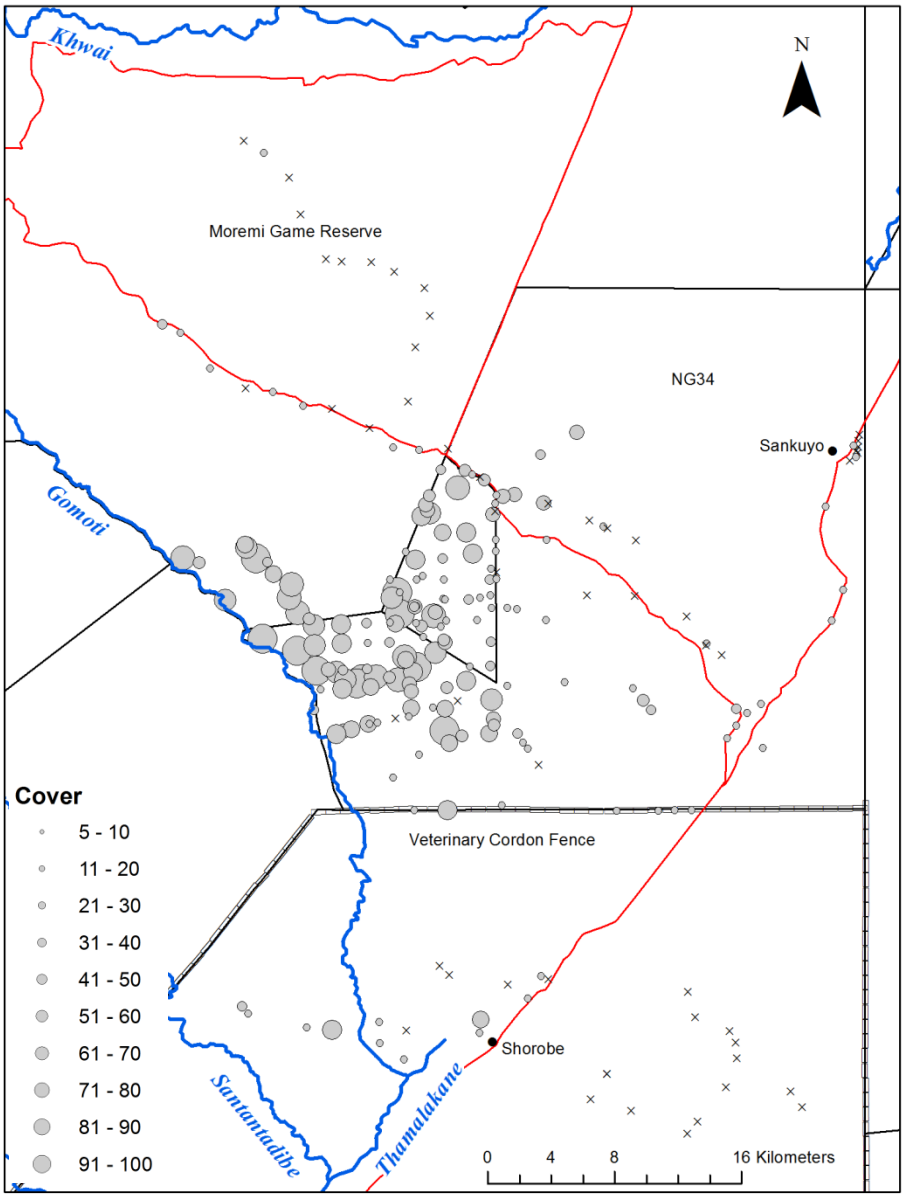

Figure 6.4: Geographic extent of aerial cover of *Pecheul-Loeschea leubnitziae* at all samples sites with large circles indicating extensive cover and small symbols indicating minimal cover. Crosses indicate an absence of *Pecheul-Loeschea leubnitziae*. Roads are indicated in red and rivers in blue.

6.4 DISCUSSION

There was no effect of type of land utilization on the likelihood of occurrence of *P. leubnitziae*, despite the species being considered to be an indicator of overgrazed and trampled areas (Burke 2000, Strobach 2001). A very hot fire (FDI = 61 – 75) also appears to have little to no effect on the likelihood of occurrence of *P. leubnitziae*. Contrary to our findings Heinl (2007) noted that the cover of *P. leubnitziae* increased with increasing time since the last burn. This difference may however be due to the fact that the

burnt areas sampled in this study had only been burnt once, two years prior to sampling. As *P. leubnitziae* is a multi-stemmed species (Roodt 1998) with a thickened underground root stock it has a fairly high fire survival rate. The thickened root stock allows the species to coppice after burning, replacing the aboveground biomass destroyed by the fire. This recovery may however be dependent on the intensity of the fire as plants subjected to a cool fire have been observed to coppice fairly successfully, while plants subjected to a more intense fire showed significantly less coppice growth (Trollope 2007).

The predominant factor affecting the occurrence of *P. leubnitziae* was found to be VMU, with the likelihood of *P. leubnitziae* occurrence being low in the *Colophospermum mopane* dominated VMUs, tall mopane woodland and shrub mopane woodland, and high in mixed thornveld and mixed broadleaf woodland. The reasons for this are two-fold. Firstly tall mopane woodland and shrub mopane woodland tend to have a higher total woody density than mixed thornveld and mixed broadleaf woodland, another factor which was found to have a significant effect of the occurrence of *P. leubnitziae*. As established woody species create a zone of resource depletion around them it would be expected that a region with a high total woody species density would not only have limited available soil resources but that established plants would also limit available light resources through shading (Smith and Walker 1983, Smith and Goodman 1986). This however does not explain the low likelihood of occurrence at low total woody species densities in tall mopane woodland and shrub mopane woodland. The absence of *P. leubnitziae* in these two VMUs is more likely to be as a result of species composition than total woody species density, while in mixed thornveld and mixed broadleaf woodland the total woody species density appears to be a more influential factor. As *C. mopane* is a dominant species in both tall mopane woodland and shrub mopane woodland and largely absent in mixed thornveld and mixed broadleaf woodland it is likely that the absence of *P. leubnitziae* can be attributed to the presence of this species. *Colophospermum mopane* is an extremely strong belowground competitor (Smit and Rethman 1998, Rathogwa et al. 1999) with approximately 66% of its fine root biomass in the top 40cm of the soil (Smit and Rethman 1998). This intense competition is the reason for the sparse grass layer seen in most mopane woodlands (Teshirogi 2010) and is likely to contribute to the absence of *P. leubnitziae* in tall mopane woodland and shrub mopane woodland. By contrast the root distribution in *Acacia* savanna is fairly even (Knoop and Walker 1985). Other studies have noted a lack of competition between the canopy microphyllous and understory broadleaf components in *Acacia* savanna (Smith and Walker 1983, Smith and Goodman 1986). The first 10cm of the soil profile in broadleaf communities tends to be dominated by herbaceous plant roots, while the woody plant roots dominate the profile between 10 and 60cm (Knoop and Walker 1985). This lack of woody root density in the upper sections of the soil profile (Knoop and Walker 1985) coupled with the low grass basal cover in mixed broadleaf woodland allows for the establishment of stands of *P.*

leubnitziae. Owing to the strong effect of VMU on likelihood of *P. leubnitziae* occurrence it is possible that the lack of effect of type of land utilization may be due to the fact that the grazing areas in Sankuyo and more than half the grazing areas in Shorobe were located in shrub mopane woodland.

Interestingly soil sand content and soil pH had no effect on the likelihood of occurrence of *P. leubnitziae*. It is however possible that other soil variables, such as organic matter content which increases the levels of insoluble cations such as, phosphorus, calcium and magnesium (Bonyongo and Mubyana 2004) may have some effect on *P. leubnitziae* likelihood of occurrence as the species tends to colonise drying floodplains (Huntsman-Mapila et al. 2003, Murray-Hudson 2009) rich in decaying plant material deposited by the floodwaters (Bonyongo and Mubyana 2004). The geographic distribution of *P. leubnitziae* in NG33, NG34 and Moremi Game Reserve supports this as the species is most abundant in the dry floodplain regions east of the Gomoti River. In the early 1900s this river was a major outflow from the Delta (Bernard and Moetapele 2005) and much of the surrounding area was swampy and regularly flooded (Rűbbel and Child 1976, Johnson and Bannister 1977, McCarthy and Ellery 1994, Ellery and McCarthy 1998). The water levels in the Gomoti River began to decrease in the 1950s (Bernard and Moetapele 2005) and by the late 1980s the floodplains had begun to dry (McNutt 2009).

6.5 CONCLUSIONS

As *Pecheul-Loeschea leubnitziae* tends to form tall monotypic stands in sparse savanna and dry grassland decreasing the available grazing for grassland herbivores, decreasing the visibility for photographic safaris and potentially facilitating ingress of woody plants in grasslands. For these reasons the development of a *P. leubnitziae* management plan to decrease the abundance of the species in areas where it dominates and to alter the height structure of the stands, decreasing the overall height, will both increase the available grazing and improve visibility in term of photographic safaris and wildlife tourism.

The findings of Trollope (2007) and Heinl (2007) indicate that further investigation into the effects of fire on *P. leubnitziae* in mixed thornveld and mixed broadleaf woodland, the two VMUs vulnerable to colonisation by this species, is warranted. While our study shows that a single fire event had no significant effect on the cover of *P. leubnitziae* the observations made by Trollope (2007) indicate that the intensity of the burn may affect the coppicing success of the *P. leubnitziae* shrubs. For the control of bush encroachment a high intensity surface head fire is recommended (Trollope 1974). The conditions required for this type of fire are as follows; air temperature >25°C, relative humidity <30%, fuel load >3000 kg/ha and fuel moisture <40% (Trollope 1980). While burning under these conditions will effectively reduce the aerial cover of *P. leubnitziae*, it may not affect the root stock. It is possible that repeated burning may also

reduce the coppicing success of the *P. leubnitziae* shrubs by depleting the stored resources in the thickened root stock.

For this reason the effects of repeat burning on the survival of *P. leubnitziae*, coupled with the effects of burning on *P. leubnitziae* seed production, seed germination (Trollope 2007) and the level of vegetative reproduction by means of runners from mature plants (Davies and Waite 1998) need to be investigated before a comprehensive management plan can be developed.

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CHAPTER 7 : THE INFLUENCE OF *PECHEUL-LOESCHEA LEUBNITZIAE* ON GRASS SWARD AND SEED BANK COMPOSITION

7.1 INTRODUCTION

Soil seed banks are the vestigial remains of historical vegetation composition at a particular site (Hopfensperger 2007). The species contained within them have the potential to become components of the future vegetation composition, provided that germination conditions are suitable (Davies and Waite 1998). The composition of seed banks may differ somewhat from that of the present and historical above-ground vegetation as a result of the longevity of the seeds within them. In general perennial species tend to produce short-lived seeds, while annual species and species adapted to nutrient-poor environments produce longer-lived seeds (Bossuyt et al. 2006, Jacquemyn et al. 2011) and these seeds play a vital role in the recovery of the plant community after disturbance (Coffin and Lauenroth 1989). Historically much of the work on seed banks has been focused on the problem of agricultural weeds (Coffin and Lauenroth 1989, Davies and Waite 1998). However, in the last decade this focus has shifted towards conservation of extant vegetation and rehabilitation of regions degraded by agricultural use and re-vegetation after disturbances such as shrub removal and drought, eg. (Davies and Waite 1998, Wagner et al. 2003, Luo and Wang 2006, Jacquemyn et al. 2011).

The level of similarity between aboveground vegetation and the seedbank has been found to be the highest in grasslands (54 %), and lowest in forest systems, (31 %) (Hopfensperger 2007). High levels of disturbance and unpredictable growing conditions result in a persistent seed bank often dominated by annuals which leads to high levels of similarity between the seed bank and the aboveground vegetation (Hopfensperger 2007, Caballero et al. 2008). This similarity decreases over successional time possibly due to an increase in woody shrubs in the aboveground vegetation (Hopfensperger 2007) which do not generally form part of the persistent seed bank because they often rely on vegetative not sexual reproduction (Thompson and Grime 1979, Davies and Waite 1998, Albrecht et al. 2011). One such woody species which dominates large areas in the drier regions of the Okavango Delta is *Pecheul-Loeschea leubnitziae*. It is a multi-stemmed, aromatic shrub of approximately 1.4 m in height. It colonizes sandy, alkaline soils favouring those with saline ground water and is common in the open woodland and grassland regions, often occurring in disturbed areas. It has composite flower heads which produce large quantities of small, wind distributed seeds (Ellery and Ellery 1997, Roodt 1998). Other than several observations that the species tends to colonise overgrazed and trampled areas, little is known about its role in grassland succession, its population demographics, seed biology and the role seed banks play in this (Burke 2000, Strohbach and Cole 2007). Field observations indicate that *P. leubnitziae* may facilitate

the succession of grassland to woody species such as *Combretum hereroense* and *Acacia erioloba* culminating in well developed woodland characterised by large *A. erioloba* trees (Trollope 2007 personal communication). Several other studies have observed pioneer shrubs to play a critical role in the succession of grassland to savanna and woodland. While the majority have found these pioneer species to act as facilitators to woody species establishment (Vieira et al. 1994, Li and Wilson 1998, Kuiters and Slim 2003, Dalton 2007) some species such as Bracken Fern (*Pteridium aquilinum*) have been observed to have the opposite effect, retarding woody development by increasing fire intensity and thus increasing woody seedling mortality (Adie et al. 2011). In order to fully understand the dry savanna and woodland regions of the Okavango Delta, an understanding of the population dynamics of *P. leubnitziae* and the role it plays in grassland succession is essential.

The objective of this chapter was to determine the following; (1) the correlation between seedbank and aboveground vegetation characteristics (2) the influence of above ground cover of *Pecheul-Loeschea leubnitziae* on relative abundance of grass species within the seedbank, (3) the effect of *Pecheul-Loeschea leubnitziae* above ground cover on species composition of above ground vegetation and (4) the influence of aboveground of *Pecheul-Loeschea leubnitziae* cover on relative proportions of grasses and non-grass species within a seed bank.

7.2 METHODS

7.2.1 Data Collection

Seed banks were studied in semi-arid thornveld and mopane savanna in the concession area NG34 in the south-eastern region of the Okavango Delta, Botswana. In May 2010 topsoil samples were collected at 104 sites with differing aboveground cover of *Pecheul-Loeschea leubnitziae*. These sites were 50m x 50m in size and were located a minimum of 1km apart. Cover categories ranged from 0 to 90 percent cover and increased in increments of 10 %. At each site five sub-samples were collected a minimum of 10m apart and combined as one site sample. Each sub-sample covered an area of approximately 20cm x 20cm and was collected from the top 10cm of the topsoil layer. The number of sample sites for each cover category ranged from eight to eleven with a total number of 104 samples. In mid-October 2010 these samples were spread out in 300 x 150 mm plastic trays lined with paper towel, to prevent the loss of sand and seed material through holes in the bottom of the trays. Soil depth in the trays was approximately 2cm. The trays received natural rainfall and were irrigated daily. The germinating seedlings were photographed, given codes and a written description and representative specimens transplanted for identification at maturity. Seedlings were counted and removed from the trays every week until germination stopped after eight weeks.

Aboveground species abundance was visually estimated using a 50m x 50m plot in which grass species composition and abundance and cover percentage of *Pecheul-Loeschea leubnitziae* was estimated and expressed as relative abundance.

7.2.2 Data Analysis

A Mantel Test with a Bray-Curtis distance measure conducted in PC-ORD (McCune and Mefford 1997) was used to determine the level of correlation between the seed bank and the aboveground vegetation and a Canonical Correspondence Analysis conducted in CANOCO (ter Braak and Smilauer 1997) to determine if the aboveground cover of *P. leubnitziae* differentially affected (a) the relative abundance of grass species within the seedbank and (b) grass species composition aboveground. Regression analysis conducted in Microsoft® Office Excel® (Microsoft-Corporation 2006) was used to determine if the aboveground cover of *P. leubnitziae* affected the relative proportions of grass and non-grass species within the seed bank.

7.3 RESULTS

The Mantel Test revealed no correlation between the composition of the seedlings that germinated from the seed bank and aboveground species composition ($r = 0.034$, $p = 0.209$). Of the 9400 germinations over the eight week trial period, only six grass species were observed of which four were perennial and two were annual species. The dominant species in the seed bank were the perennials *Urochloa mosambicensis* (57% ± 3.0) and *Panicum maximum* (17% ± 2.2) and the annual species *Dactylotenium gigantium* (8% ± 1.6) (Table 7.1). A total of 23 grass species were observed in the sward, of which 18 were perennial and five were annual. Five species were common to both the seedbank and the aboveground vegetation, namely *Urochloa mosambicensis, Chloris virgata, Panicum maximum, Dactylocenium gigantium* and *Melinis repens* (Table 7.1 and Table 7.2). *Eragrostis gummiflua* was found in low densities in the seedbank but was not recorded in the sward. It does however occur in localised patches elsewhere in the study area closely associated with waterlogged conditions. The dominant species observed in the aboveground vegetation were the perennials *U. mosambicensis* (12% ± 1) and *Eragrostis lehmanniana* (16% ± 2) and the annual species *D. gigantium* (14% ± 1) (Table 7.2).

Table 7.1: Relative abundance of species contributing to the seedbank under differing levels of *P. leubnitziae* cover. Species abbreviations are explained in Appendix B

	Pecheul-Loeschea leubnitziae cover (%)										
	0	10	20	30	40	50	60	70	80	90	Total
CVI	6 ± 9	4 ± 7	11 ± 17	19 ± 33	4 ± 6	2 ± 5	8 ± 22	9 ± 17	2 ± 3	4 ± 8	7 ± 1
DGI	14 ± 22	5 ± 8	2 ± 3	14 ± 33	4 ± 7	13 ± 19	2 ± 5	11 ± 12	3 ± 6	9 ± 16	8 ± 2
EGU	2 ± 5	1 ± 2	3 ± 5	6 ± 17	2 ± 5	0 ± 0	1 ± 3	3 ± 6	0 ± 0	6 ± 13	2 ± 1
FORB	8 ± 15	7 ± 8	5 ± 7	16 ± 28	8 ± 13	3 ± 5	6 ± 7	3 ± 9	8 ± 18	4 ± 10	7 ± 1
MRE	1 ± 2	0 ± 1	1 ± 2	0 ± 0	5 ± 7	1 ± 3	0 ± 1	12 ± 26	4 ± 6	2 ± 5	3 ± 1
PMA	24 ± 30	18 ± 27	8 ± 10	12 ± 20	33 ± 22	22 ± 20	13 ± 22	9 ± 20	13 ± 14	16 ± 17	17 ± 2
UMO	46 ± 32	65 ± 28	70 ± 22	34 ± 39	45 ± 31	59 ± 23	70 ± 27	53 ± 33	70 ± 23	59 ± 29	57 ± 3

Table 7.2: Relative abundance of species contributing to the grass sward under differing levels of *P. leubnitziae* cover. Species abbreviations are explained in Appendix B

	Pecheul-Loeschea leubnitziae cover (%)										
	0	10	20	30	40	50	60	70	80	90	Total
ACO	1 ± 2	0 ± 2	0 ± 0	4 ± 8	3 ± 6	3 ± 7	3 ± 6	4 ± 9	3 ± 4	3 ± 7	2 ± 1
AJU	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	1 ± 2	1 ± 3	0 ± 0	0 ± 0	0 ± 0	0 ± 0
AME	0 ± 0	2 ± 6	0 ± 0	0 ± 0	1 ± 2	4 ± 9	5 ± 10	8 ± 13	0 ± 0	1 ± 2	2 ± 1
CCI	0 ± 0	1 ± 3	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
CDA	15 ± 21	8 ± 18	10 ± 18	7 ± 17	7 ± 14	9 ± 17	3 ± 10	3 ± 8	13 ± 23	5 ± 10	8 ± 2
CVI	5 ± 8	6 ± 10	6 ± 12	18 ± 20	14 ± 16	1 ± 3	8 ± 11	6 ± 13	11 ± 14	3 ± 9	8 ± 1
DER	7 ± 10	9 ± 12	11 ± 13	7 ± 13	12 ± 13	11 ± 13	8 ± 6	4 ± 7	6 ± 13	11 ± 17	9 ± 1
DGI	8 ± 13	19 ± 14	16 ± 14	4 ± 6	13 ± 12	16 ± 18	14 ± 11	14 ± 12	14 ± 20	20 ± 13	14 ± 1
ECL	0 ± 1	0 ± 0	0 ± 0	1 ± 2	0 ± 0	0 ± 0	2 ± 5	0 ± 0	0 ± 0	0 ± 0	0 ± 0
EEC	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	1 ± 3	0 ± 0
EGU	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
ELE	19 ± 23	14 ± 10	32 ± 23	17 ± 13	22 ± 14	10 ± 16	11 ± 12	12 ± 17	11 ± 14	10 ± 13	16 ± 2
ERI	12 ± 23	1 ± 3	0 ± 0	3 ± 10	1 ± 3	6 ± 16	0 ± 0	4 ± 10	3 ± 9	0 ± 0	3 ± 1
HDI	0 ± 0	0 ± 0	1 ± 2	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.1 ± 0
MRE	0 ± 0	2 ± 4	1 ± 2	0 ± 0	0 ± 0	6 ± 10	3 ± 6	5 ± 8	1 ± 2	3 ± 6	2 ± 1
PMA	11 ± 16	10 ± 10	11 ± 11	6 ± 10	7 ± 8	7 ± 10	6 ± 4	9 ± 13	6 ± 9	15 ± 16	9 ± 1
PSQ	2 ± 5	6 ± 14	1 ± 2	6 ± 11	11 ± 17	10 ± 11	4 ± 12	10 ± 19	8 ± 13	14 ± 17	7 ± 1
SFE	2 ± 5	3 ± 6	0 ± 0	3 ± 10	1 ± 3	0 ± 0	2 ± 5	0 ± 0	0 ± 0	0 ± 0	1 ± 1
SHI	3 ± 7	0 ± 2	0 ± 0	8 ± 18	5 ± 13	6 ± 10	6 ± 13	6 ± 10	4 ± 8	5 ± 6	4 ± 1
SIO	0 ± 0	0 ± 0	0 ± 0	5 ± 11	0 ± 0	0 ± 0	0 ± 0	0 ± 0	1 ± 3	1 ± 3	1 ± 0
SKA	3 ± 10	1 ± 5	0 ± 0	1 ± 2	0 ± 0	1 ± 3	12 ± 26	0 ± 0	9 ± 28	2 ± 5	3 ± 1
SVE	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	1 ± 3	1 ± 2	0 ± 0	1 ± 3	0 ± 0	0 ± 0
UMO	10 ± 15	19 ± 16	12 ± 15	11 ± 23	6 ± 7	12 ± 13	11 ± 11	18 ± 11	11 ± 18	10 ± 16	12 ± 2

The aboveground cover of *P. leubnitziae* had no effect on the relative abundance of species within the seed bank (Monte Carlo test of CCA axis 1: p = 0.31). Regression analysis showed no significant linear (or apparent non-linear) effect of aboveground cover of *P. leubnitziae* on the proportion of grass and forb species in the seedbank (p = 0.308, r^2 = 0.010, SE = 13.486) (Table 7.3). In addition, *P. leubnitziae* did not germinate from the seed bank, irrespective of the size of its population in the sward.

Table 7.3: Analysis of variance for regression analysis on the proportion of grass and forb species in the seedbank under different levels of *P. leubnitziae* cover

	df	SS	MS	F	p-value
Regression	1	190.62	190.62	1.058	0.308
Residual	102	18552.13	181.88		
Total	103	18742.75			

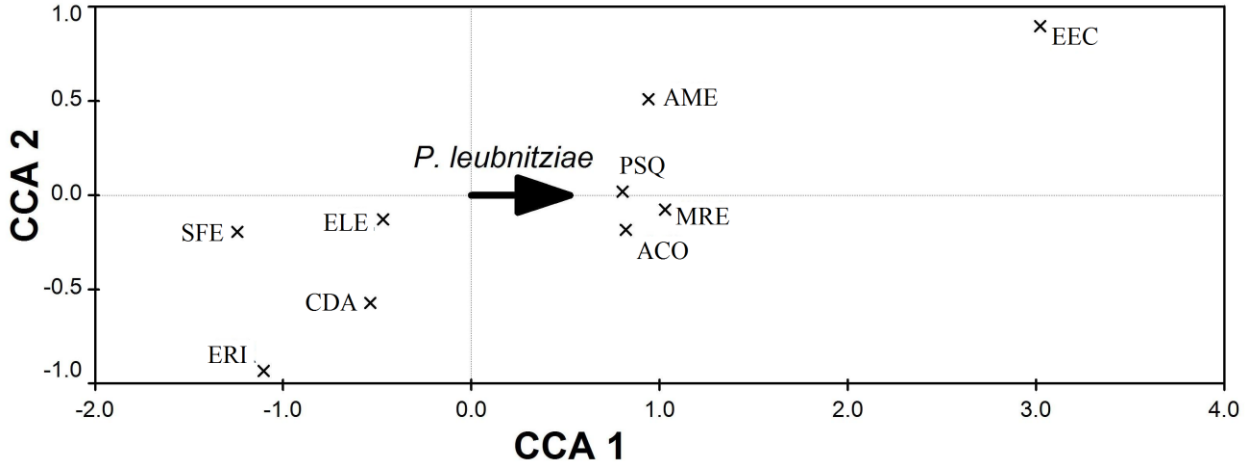

Figure 7.1: Canonical correspondence analysis (CCA) of the effect of *Pecheul-Loeschea leubnitziae* cover (%) on proportional above-ground grass composition (p = 0.018). Species with <1% of their variance accounted for by CCA axis 1 are not shown. Species abbreviations are explained in Appendix B.

Cover of *P. leubnitziae* was found to significantly influence aboveground grass species composition (Figure 7.1). Two distinct species groupings were formed at low and high *P. leubnitziae* cover. Sites with a low cover of *P. leubnitziae* had a higher abundance of *Eragrostis rigidior, Cynodon dactylon, E. lehmanniana* and *Sporobolus festivus*, while sites with high cover of *P. leubnitziae* were characterized by *Aristida meridionalis, Pogonarthria squarrosa, Melinis repens* and *Aristida congesta*. *Eragrostis echinocloidea* occurred at very low densities in the sites with a 90% cover of *P. leubnitziae.*

7.4 DISCUSSION

Savannas generally consist of patches where varying densities of trees are co-dominant with a continuous herbaceous layer within a grassland matrix (Sankaran et al 2005). Grassland communities generally have a high level of similarity between the aboveground vegetation and the seedbank (Hopfensperger 2007), however in this study there was almost no correspondence. Similar observations were made by Coffin & Laurenroth (1989) and Perez et al (1998). This is not entirely surprising as high annual variability has been observed in the aboveground vegetation and seedbank in arid environments (Caballero et al. 2008). Grasslands with a high similarity between the seed bank and vegetation are often highly disturbed or located in regions with unpredictable growing conditions (Hopfensperger 2007), resulting in a dominance of annuals (Caballero et al. 2008), or are overgrazed and thus have low seed production (Bossuyt et al. 2006). In addition the time of year during which studies took place may affect results as seedbank to aboveground vegetation similarity has been found to be highest during autumn (Kemeny et al. 2005).

Five times more perennial grass species were observed in the aboveground grass sward than in the seed bank whereas only double the number of annual species was observed. This could be explained by the fact that most perennial species produce seeds which are only viable for short periods while annual species and species which favour nutrient-poor environments produce longer-lived seeds (Bossuyt et al. 2006, Jacquemyn et al. 2011). *Urochloa mosambicensis* is one of the most dominant species in the seed bank, representing more than half the germinable seed bank but only 12 percent of the aboveground grass sward. Its overrepresentation in the seed bank may be due to the fact that it produces large numbers of small seeds (Erikson and Erikson 1997). The perennial, *Panicum maximum* exhibits a similar trend, contributing 17 percent to the seed bank and only nine percent of the aboveground grass sward. No germination on *P. leubnitziae* was observed in any of the seedbank samples regardless of the aboveground cover of the shrub. It is therefore likely that this species is reproducing vegetatively by means of suckers or runners from mature plants rather than by contributing to the germinable seedbank (Davies and Waite 1998).

P. leubnitziae population had no effect on the relative abundance of species in the seed bank, or to the ratio of grass to non-grass species in the seed bank, however it was found to have an effect on the aboveground grass sward species composition. Where *P. leubnitziae* was sparse; short grasses with narrow leaves (eg. *Eragrostis rigidior, Cynodon dactylon, Eragrostis lehmanniana* and *Sporobolus festivus*) predominate, while only shade tolerant species (eg. *Aristida meridionalis, Pogonarthria squarrosa, Melinis repens* and *Aristida congesta*) were found under dense populations of *P. leubnitziae* (Chippindall and Crook 1976, Gibbs Russell et al. 1991, Veenendaal et al. 1993, van Oudtshoorn 1999).

All four species characteristic of sites with high *P. leubnitziae* cover have low grazing value, while three of the four species characteristic of sites with low *P. leubnitziae* cover have average to good grazing value (van Oudtshoorn 1999) indicating that the encroachment of *P. leubnitziae* may be concomitant with a decrease in veld quality and hence a reduction in land use potential.

7.5 CONCLUSION

Although *P. leubnitziae* cover in semi-arid thornveld and mopane veld influenced grass sward composition with an increase in poor quality, shade tolerant species with increasing *P. leubnitziae* cover it had no effect on seed bank composition and was itself not apparent in the seedbank. This exploratory study highlights the dearth of information regarding not only the reproductive strategy of *P. leubnitziae* but also its response to environmental drivers. As *P. leubnitziae* covers extensive areas within both the community grazing lands and the wildlife management area, an understanding of the species response under different management strategies, grazing schemes and fire regimes, as well as an understanding of its life history and population demographics is essential for both wildlife conservation and livestock management. As a pioneer species within these dry savanna and woodland regions further study to facilitate a better understanding of *P. leubnitziae* is strongly recommended.

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CHAPTER 8: DRY WOODLAND AND SAVANNA VEGETATION DYNAMICS: A SYNTHESIS

The dry woodland and savanna regions on the periphery of the Okavango Delta have been largely overlooked in terms of their species composition, structure, density and response to environmental drivers. Most broad vegetation classifications divide the woodland into *Acacia* dominated woodland and mopane dominated woodland (Mendelsohn and el Obeid 2004) (Figure 8.1). Research conducted elsewhere in Africa indicates distinct structural differences between *Colophospermum mopane* woodlands on damp, nutrient rich soils and dry, nutrient poor soils (February et al. 2007), however neither of the more commonly used broad vegetation classifications mention this, referring to mopane woodland as a single category (Jellema et al. 2002, Mendelsohn and el Obeid 2004).

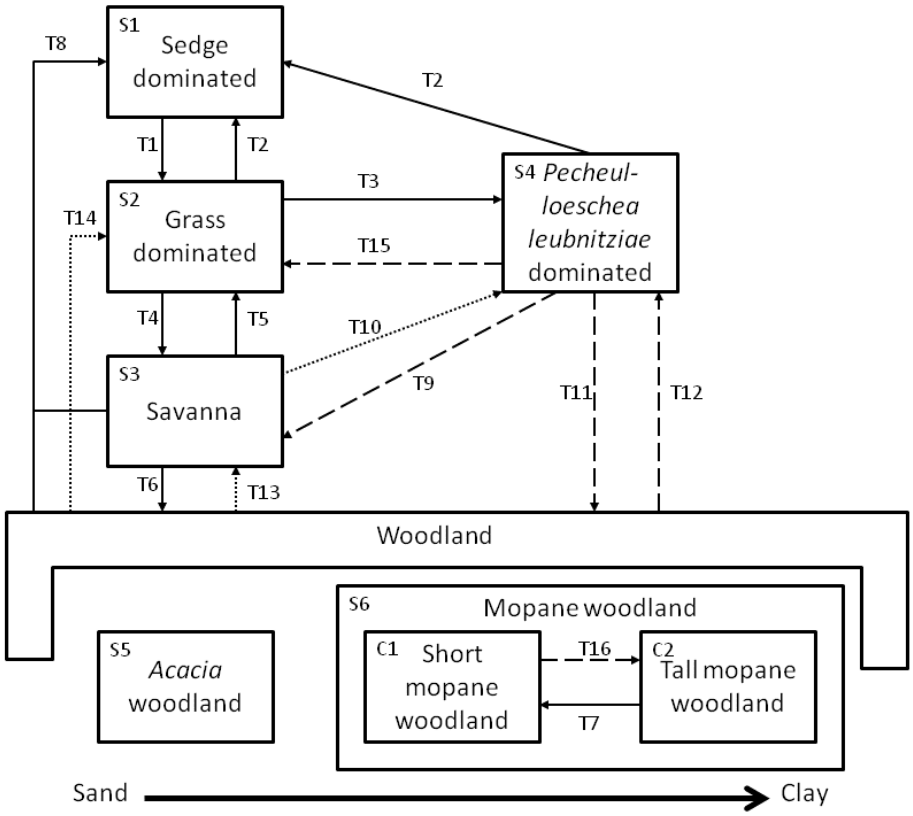

Figure 8.1: Okavango Delta terrestrial vegetation state and transition model. S indicates states, T indicates transitions between states and C indicates plant communities. Solid lines indicate well documented transitions, dotted lines indicate transitions which may be inferred from previous research and the dashed lines indicated transitions for which no data were available. Transitions are explained in Table 8.1.

Table 8.1: Vegetation transitions for the Okavango Delta terrestrial vegetation

Transition	Main Causes
T1	Decrease in flooding frequency to every 2 to 5 years
T2	Annual flooding
T3	Flooding stops and area is heavily grazed/disturbed
T4	Decrease in flooding frequency to every 5 to 10 years
T5	Biennial fire, woody utilization (e.g. Elephants/Wood harvesting)
T6	No flooding, infrequent burning (every 5 years+), little utilization
T7	Fire, woody utilization (e.g. Elephants/Wood harvesting)
T8	Annual flooding
T9	No data
T10	Heavy utilization and disturbance
T11	No data
T12	No data
T13	Fire, woody utilization (e.g. Elephants/Wood harvesting)
T14	Fire, woody utilization (e.g. Elephants/Wood harvesting)
T15	No data
T16	No data

The seasonal floodplains of the Okavango Delta have been extensively researched (Bonyongo and Mubyana 2004, Heinl 2005, Murray-Hudson 2009) however there has been little focus on the species composition, response to environmental factors and successional changes on floodplains which have been dry for extended periods and the dry woodlands adjoining them.

This thesis provides a more comprehensive description of the various woodland and savanna states on the eastern periphery of the Okavango Delta and the plant communities within them, as well as their response to anthropogenic utilization and fire. The *Acacia* woodlands referred to by Mendelsohn and el Obeid (2004) can be more accurately referred to as a savanna state, 'a continuous grass layer with scattered trees' (Scholes and Archer 1997), as the woody density is somewhat lower than the woodland regions examined and the grass layer is more extensive. Within these mixed thornveld (S4) savanna regions, four plant communities (C1 to C4) (Figure 8.2) were observed, representing savannas of varying species composition and density. These four plant communities can be grouped in pairs in terms of species composition with two plant communities (C1 and C2) representing *Acacia erioloba* dominated savanna, and two representing mixed *Acacia* savanna (Figure 8.2). These savannas occur on fairly nutrient poor, sandy soils. Community pathway P1 represents the transition from open vegetation to dense, closed vegetation (Figure 8.2 and Table 8.3). Provided there are no natural or anthropogenic factors acting on the vegetation, this will occur naturally over time. The closed savanna communities could be considered as the start of a transitional vegetation state towards a woodland state, as woodland will develop if no action is taken. It is however possible to return these closed savannas to their open state through burning

(Trollope 1980), or utilization of the woody component by wildlife, such as elephants (Styles and Skinner 2000), or by the manual removal of trees through wood harvesting (Hannah et al. 1997). However once this state has progressed to a woodland state (T6) (Figure 8.2) it becomes increasingly difficult to return to savanna. Burning becomes less effective as the extent of the grass layer is diminished, thus reducing the available fuel load (Trollope 1980), leaving only utilization of the woody layer as an effective, albeit time-consuming method of tree removal (T13) (Figure 8.2).

The dry woodland component of the vegetation was found to be comprised of three states, the presence of which is dependent on the underlying soils (Figure 8.2). The two morphologically different forms of mopane described by February et al. (2007) were observed with the short form, shrub mopane woodland (S6) having only one plant community, short mixed mopane woodland (C9), while the taller form, tall mopane woodland (S7) had two plant communities, tall mixed mopane woodland (C10) and tall pure mopane woodland (C11). There is currently no data available on the community pathway between these two states (C6) (Figure 8.2), however it is possible that utilization of the woody layer will result in a decrease in the strong belowground competitive effect of the tall *C. mopane* trees (Smit and Rethman 1998), creating a niche for other species to establish. It is unlikely that shrub mopane woodland on dry, nutrient poor soils will transition to tall mopane woodland, however tall mopane woodland will become shrub mopane woodland as a result of woody layer utilization and burning, resulting in coppice growth (T7) (Figure 8.2 and Table 8.2). These regions should revert back to their tall mopane state if the factors impacting the vegetation are removed; however this may depend on the duration over which the impact occurred and soil water availability. This research has also confirmed that if soil conditions are suitable livestock utilization dominated by grazers in shrub mopane woodland will result in the development of tall mopane woodland through bush encroachment and sward-overutilization (T16) (Figure 8.2 and Table 8.2), a transition which was previously undocumented (Figure 8.1).

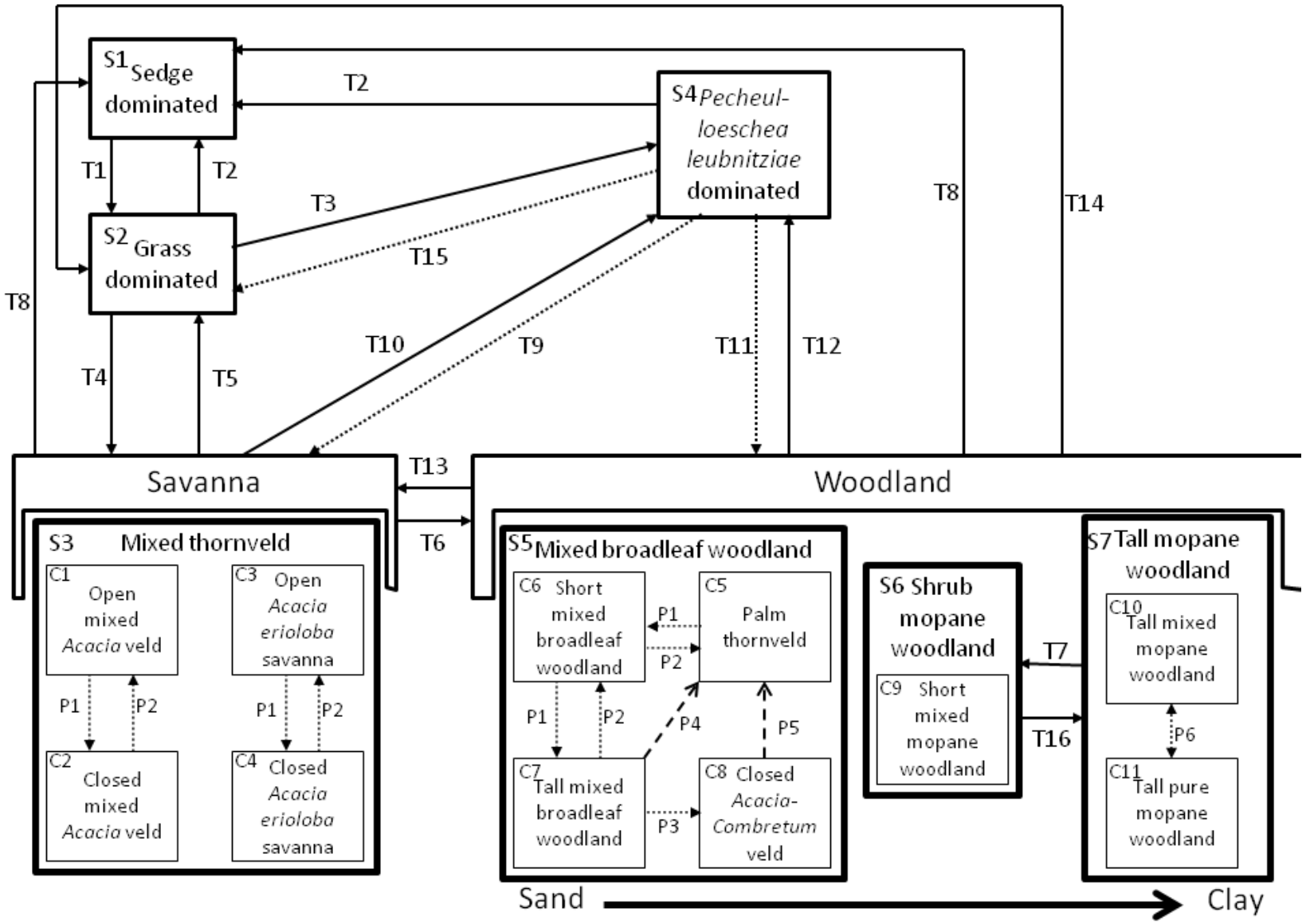

Figure 8.2: Revised Okavango Delta terrestrial vegetation state and transition model. S indicates states, T indicates transitions between states, C indicates plant communities and P indicates community pathways. Solid lines indicate well documented transitions, dotted lines indicate transitions which may be inferred from previous research and the dashed lines indicated transitions for which no data was available. Transitions are explained in Table 8.2 and community pathways in table 8.3.

Table 8.2: Revised vegetation transitions for the Okavango Delta terrestrial vegetation.

Transition	Main Causes
T1	Decrease in flooding frequency to every 2 to 5 years
T2	Annual flooding
T3	Flooding stops
T4	Decrease in flooding frequency to every 5 to 10 years
T5	Biennial fire, woody utilization (e.g. Elephants/Wood harvesting)
T6	No flooding, infrequent burning (every 5 years+), little utilization
T7	Increased fire or woody utilization (e.g. Elephants/Wood harvesting)
T8	Annual flooding
T9	Possibly repeated, high-intensity burning, a single short duration flood or inundation resulting from extended rainfall
T10	No action
T11	Possibly repeated, high-intensity burning, a single short duration flood or inundation resulting from extended rainfall
T12-S5	No action or natural succession
T12-S6&7	Invasion unlikely
T13-S5	Increased burning and woody utilization (e.g. Elephants/Wood harvesting)
T13-S6&7	Increased woody utilization (e.g. Elephants/Wood harvesting)
T14-S5	Increased fire and woody utilization (e.g. Elephants/Wood harvesting)
T14-S6&7	Increased flooding frequency
T15	Possibly repeated, high-intensity burning, a single short duration flood or inundation resulting from extended rainfall
T16	Removal of fire and woody utilization. Over-utilization by grazing livestock leading to bush encroachment

Table 8.3: Community pathways for the Okavango Delta terrestrial vegetation

Community Pathway	Main Causes
P1	No action or natural succession
P2	Burning or utilization of woody layer (elephants/harvesting)
P3	*Combretum* species protected from elephant utilization
P4	No data
P5	No data
P6	No data

Mixed broadleaf woodland (S5) comprises of four plant communities, palm thornveld (C7), short mixed broadleaf woodland (C5), tall mixed broadleaf woodland (C6) and closed *Acacia-Combretum* veld (C8). It is possible that these four communities form a succesional pathway on old floodplains with palm thornveld developing after floodplains have dried, followed by the development of short and tall broadleaf woodland as more woody species colonise the dry floodplains. The final community following the development of tall broadleaf woodland would be closed *Acacia-Combretum* woodland. The dominance of *Combretum* species in this late

successional broadleaf community is as a result of the vegetation density. These species are heavily utilized by elephants (Roodt 1998) and the dense vegetation in closed *Acacia-Combretum* woodland provides protection from elephant utilization (P3) (Table 8.3). No data was available regarding the transition from tall mixed broadleaf woodland and closed *Acacia-Combretum* woodland back to palm thornveld (P4 and P5). However tall mixed broadleaf woodland should revert back to short mixed broadleaf woodland (P2) and short mixed broadleaf woodland should return to palm thornveld (P2) as a result of repeated burning as one of the dominant species in these two vegetation communities, *Croton megalobotrys*, is negatively affected by fire (Table 8.3).

Flooding is known to have a negative effect on woody species, thus it follows that extended and repeated flooding in the woodland regions will result in sedge dominated floodplain vegetation (T8) (Figure 8.1 and Table 8.1). However this research has shown that it is unlikely that the mopane dominated woodland regions will revert to grass dominated vegetation. This is not the case for mixed broadleaf woodland as the burning decreases canopy cover by removing *C. megalobotrys* allowing the grass sward to develop. In this state repeated burning over a number of years will result in largely grass dominated vegetation (T14) (Figure 8.2 and Table 8.2).

Pecheul-loeschea leubnitziae is a shrubby pioneer species which was found have an extensive distribution in the dry woodland and savanna regions of the eastern Okavango Delta. Little is known about the species, however it is generally considered to be an indicator of dry floodplains and over-grazed, disturbed vegetation (Burke 2000, Strobach 2001, Huntsman-Mapila et al. 2003, Murray-Hudson 2009). This research found livestock utilization to have little effect on the occurrence of the species, with extensively overgrazed regions having little to no cover of *P. leubnitziae*, but rather that the presence of the species in high densities results in a sward comprised of shade-tolerant grasses with low grazing value. *Pecheul-loeschea leubnitziae* appears to colonise dryland vegetation naturally and was found to be an indicator of dry, sand dominated vegetation as it was frequently observed in mixed thornveld savanna and mixed broadleaf woodland, however it was absent in the clay dominated mopane vegetation (T12) (Figure 8.2 and Table 8.2). It is likely that this is due to a combination of the strong belowground competition exerted by the shallow fine root system of *C. mopane* and the greater soil water capacity of clay soils when compared to sandy soils. While this research found a single fire to have no effect on the occurrence of *P. leubnitziae*, it is possible that repeated, high intensity burning may negatively affect the species (Trollope 2007). In addition to this, the species is intolerant of water-logging and thus a single short flood or

inundation resulting from extended rainfall reduces *P. leubnitziae* occurrence (T9, T11 and T15) (Figure 8.2 and Table 8.2).

From this research it appears that the *C. mopane* dominated woodlands are a stable state, which is unlikely to be invaded by woody pioneer species or revert to grassland or savanna vegetation, without widespread mechanical removal of trees. Only extensive, recurring flooding appears likely to alter the state of these woodlands. Mixed thornveld savanna and mixed broadleaf woodland are less stable states, which are vulnerable to colonisation by pioneer species and can be altered as a result of burning or utilization. For this reason management and monitoring of this vegetation is essential to prevent vegetation degradation and to ensure optimal forage availability for both livestock and wildlife.

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APPENDIX A – WOODY SPECIES LIST

ADI	*Adansonia digitata*	DCI	*Dichrostachys cinerea*
AEB	*Acacia erubescens*	DLY	*Diospyros lycioides*
AER	*Acacia erioloba*	DME	*Diospyros mespiliformis*
AFL	*Acacia fleckii*	EDI	*Euclea divinorum*
AHE	*Acacia hebeclada*	ERI	*Ehritia rigida*
ALU	*Acacia luederitzii*	GBI	*Grewia bicolor*
AME	*Acacia mellifera*	GFA	*Grewia flava*
ANI	*Acacia nigrescens*	GFS	*Grewia flavescens*
ASI	*Acacia sieberiana*	GRE	*Grewia retinervis*
ATO	*Acacia tortilis*	GSE	*Gymnosporia senegalensis*
BAL	*Boscia albitrunca*	GVO	*Gardenia volkensii*
BGA	*Bauhinia galpinii*	HPE	*Hyphaene petersiana*
BMO	*Boscia mossambicensis*	KAF	*Kigelia africana*
CAF	*Commiphora africana*	LCA	*Lonchocarpus capassa*
CAL	*Catophractes alexandri*	LNE	*Lonchocarpus nelsii*
CAP	*Combretum apiculatum*	RBR	*Rhigozum brevispinosum*
CHE	*Combretum hereroense*	RTE	*Rhus tenuinervis*
CIM	*Combretum imberbe*	TPR	*Terminalia prunioides*
CME	*Croton megalobotrys*	TSE	*Terminalia sericea*
CMO	*Colophospermum mopane*	UNK	Unknown species
CMZ	*Combretum mossambicense*	XAM	*Ximenia americana*
CP	*Commiphora pyracanthoides*	XCA	*Ximenia caffra*
CTO	*Capparis tomentosa*	ZMU	*Ziziphus mucronata*

APPENDIX B – GRASS SPECIES LIST

ACO	*Aristida congesta*
ADI	*Aristida diffusa*
AJU	*Aristida junciformis*
AMA	*Acroceras macrum*
AME	*Aristida meridionalis*
BBR	*Brachiaria brizantha*
BIR	*Bothriochloa radicans*
CCI	*Cenchrus cilliaris*
CDA	*Cynodon dactylon*
CEX	*Cymbopogon excavatus*
CVI	*Chloris virgata*
CYE	*Cymbopogon excavatus*
DER	*Digitaria eriantha*
DGI	*Dactylotenium giganteum*
DIS	*Digitaria* species
DSA	*Digitaria sanguinalis*
DVE	*Digitaria velutina*
ECA	*Eragrostis capensis*
ECL	*Echinochloa colona*
ECU	*Eragrostis curvula*
EEC	*Eragrostis echinochloidea*
EGU	*Eragrostis gummiflua*
ELE	*Eragrostis lehmanniana*
EMA	*Enteropogon macrostachyus*
ENI	*Eragrostis nindensis*
ERI	*Eragrostis rigidior*
ESU	*Eragrostis superba*
EVI	*Eragrostis viscosa*
HCO	*Heteropogon contortus*
HDI	*Hyperthelia dissoluta*
HERB	Herbaceous plants
MRE	*Melinis repens*
PCO	*Panicum coloratum*
PEK	*Panicum eckloni*
PMA	*Panicum maximum*
PPA	*Perotis patens*
PRE	*Panicum repens*
PSQ	*Pogonarthria squarrosa*
SBI	*Sorghum bicolor*
SFE	*Sporobolus festivus*
SFI	*Sporobolus fimbriatus*
SHI	*Stipagrostis hirtigluma*
SIO	*Sporobolus ioclados*
SKA	*Schmidtia kalihariensis*
SSA	*Setaria sagittifolia*
SSP	*Setaria sphacelata*
SVE	*Setaria verticillata*
TBR	*Tragus berteronianus*
UMO	*Urochloa mosambicensis*
USP	*Urochloa* species